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 genus Buteo (Aves) coexisting in the prairie-parkland
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RELATIONSHIPS BETWEEN THREE SPECIES OF THE GENUS
BUTEO (AVES) COEXISTING IN THE PRAIRIE-PARKLAND
ECOTONE OF SOUTHEASTERN ALBERTA

by



JOSEF K. SCHMUTZ

A THESIS

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THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Relationships between three species of the genus *Buteo* (Aves) coexisting in the prairie-parkland ecotone of southeastern Alberta" submitted by Josef K. Schmutz in partial fulfillment of the requirements for the degree of Master of Science.

ABSTRACT

Three species of Buteoninae, ferruginous (Buteo regalis), Swainson's (B. swainsoni) and red-tailed hawks (B. jamaicensis), coexist in the prairie-parkland ecotone of southeastern Alberta. This study was designed to investigate the degree of ecological segregation between them relative to their use of food, time, space and nest sites.

All three species depended on Richardson's ground squirrels (Spermophilus richardsonii) as their main prey. The total dietary overlap between ferruginous and Swainson's hawks was 98% and 82% in the two years of this study. There was no evidence that ferruginous and Swainson's hawks partitioned their food resource either by taking different sizes or species of prey or by having different hunting methods or hunting times. There appeared to be no measurable competition for food which was abundantly available as evidenced by: similar growth rates of nestlings of both species in broods that received supplemental food and those that did not, more prey present in nests than the nestlings could eat, and an estimated proportion of less than 15% of the ground squirrel population taken by these hawks. Swainson's hawks bred later than ferruginous hawks but there was no evidence to suggest that this was a means

of reducing competition for food.

Intraspecifically, ferruginous and Swainson's hawks maintained nesting territories. Nest sites were present in excess of those used and therefore were not limiting the breeding population. Interspecifically, all three species nested in close proximity. However, chances of nesting failure increased with increasing proximity to nearest neighbor of another species, probably as a result of interspecific aggression. Therefore, competition for space containing a nest site existed and the breeding populations appeared to be limited by territorial behavior.

The distribution of nesting pairs on and outside the study area and nest site characteristics suggest that each of the three species differed in the selection of nesting habitat. Ferruginous hawks nested in trees and on the ground. Swainson's hawks nested primarily in trees and shrubs and therefore were limited to nesting where such vegetation was available. Red-tailed hawks nested only in trees of tall and dense stands. Thus, the three species apparently select different nesting habitat but their range of sympatry during the breeding season has widened through increased availability of trees in prairie habitat as the result of settlement.

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Table of Contents

Chapter	Page
INTRODUCTION	1
MATERIALS AND METHODS	4
RESULTS AND DISCUSSION	13
Natural History of the Hawks	13
Ferruginous Hawk	13
Swainson's Hawk	17
Red-tailed Hawk	19
Food Resource Overlap	20
Food Habits	21
Body Size	30
Hunting Methods	34
Hunting Times	35
Food Availability	38
Seasonal Overlap	49
Spatial Overlap	56
Territoriality	56
Interspecific Interactions	74
Nesting Success	75
Reproductive Performance	79
Growth Rates of Nestling Hawks	80
Interspecific Territoriality	84
Habitat	90

Table of Contents

Chapter	Page
Summarizing Discussion	100
Literature Cited	104
Appendices	113

List of Tables

Table	Description	Page
1.	Number of visits to hawk nests for food habit analysis	24
2.	Prey of ferruginous hawks	26
3.	Prey of Swainson's hawks	27
4.	Prey of red-tailed hawks	28
5.	Frequency of prey found in nests with augmented and unaugmented food supply	40
6.	Estimation of population density of Richardson's ground squirrels	44
7.	Comparison of estimated density of Richardson's ground squirrels with densities reported for other areas	48
8.	Correlations between reproductive performance and distances to nearest neighbors	81
9.	Correlations between reproductive performance and density of nesting pairs	82
10.	Correlations between body weight of nestlings and proximity of nesting pairs	83

List of Figures

Figure	Description	Page
1.	Study area	6
2.	Breeding ranges of the hawks	15
3.	Dietary overlap between ferruginous and Swainson's hawks	32
4.	Number of prey items found in nests in relation to time of day	37
5.	Comparison of the rate of body weight increase between nestlings with augmented and unaugmented food supply	43
6.	Chronology of breeding events of the hawks	51
7.	Distribution of hatching dates	55
8.	Location of observations of a nesting pair of Swainson's hawks	59
9.	Dispersion of nest sites on the study area	63
10.	Distances between nearest neighbors of same and different species	65
11.	Distances of nests, occupied in 1975 but not in 1976, from the nearest occupied nest	69
12.	Successful and unsuccessful nests in relation to nearest neighbor	78
13.	Responses of nesting pairs to a tethered hawk ...	87
14.	Materials used by the hawks to line their nests .	93
15.	Nest site characteristics	95
16.	Nest substratum used by the hawks	98

INTRODUCTION

In natural communities of birds many species usually coexist in the same habitat. The principle of competitive exclusion dictates ecological segregation of these species with a consequent partitioning of resources (Elton 1946, Lack 1971), a phenomenon that has been demonstrated many times (Baker and Baker 1973). Ecological segregation minimizes competition which occurs, "when an organism uses more energy to obtain (e.g. food) or maintain (e.g. living space) a unit of resource due to the presence of another individual, than it would otherwise do" (Reynoldson and Bellamy 1970:283). If ecological segregation is not possible competitive exclusion is expected to occur except in instances when unstable environments are colonized by species, when the species involved maintain mutually exclusive territories or when selective forces change repeatedly (Hutchinson 1958).

Coexisting species usually vary in the number of resources that they use in common and in the degree of dependence upon a given resource. Ecological segregation is manifested most commonly in the use of different habitats, different feeding zones within a given habitat, different kinds or sizes of food and by feeding at different times, either by staggering daily and/or seasonal activity (Cody 1974).

In southeastern Alberta, ferruginous (Buteo regalis), Swainson's (B. swainsoni) and red-tailed hawks (B. jamaicensis) coexist in the prairie-parkland ecotone. These species, besides being closely related taxonomically, have similar food habits throughout their breeding ranges, preying primarily on ground-dwelling rodents and lagomorphs (Cameron 1914, Gloyd 1925, Errington and Breckenridge 1938, Fitch et al. 1946, Hamerstrom and Hamerstrom 1954, Orians and Kuhlman 1956, Bent 1961, Angell 1969, Craighead and Craighead 1969, Luttich et al. 1970, Korschgen and Stuart 1972, Smith and Murphy 1973, Hafner 1974, McInvaille and Keith 1974, Lokemoen and Duebbert 1976). It has been suggested that ferruginous and Swainson's hawks hunt at different times of the day (Smith and Murphy 1973) and that coexistence is possible between raptors, even when the food used is similar, by hunting at different times (Cody 1974). Closely related sympatric species of raptors have been found to be ecologically segregated: six species of vultures in East Africa fed on different portions of carcasses and displayed different adaptations to do so (Kruuk 1967); falcons occupying the same habitat in Europe, differed in their feeding and hunting methods and therefore were presumed to take different prey (Lack 1971). North American and European accipiters partition their food resource by prey weight (Storer 1966, van Beusekom 1972).

How are ferruginous, Swainson's and red-tailed hawks able to coexist in southeastern Alberta? I addressed this

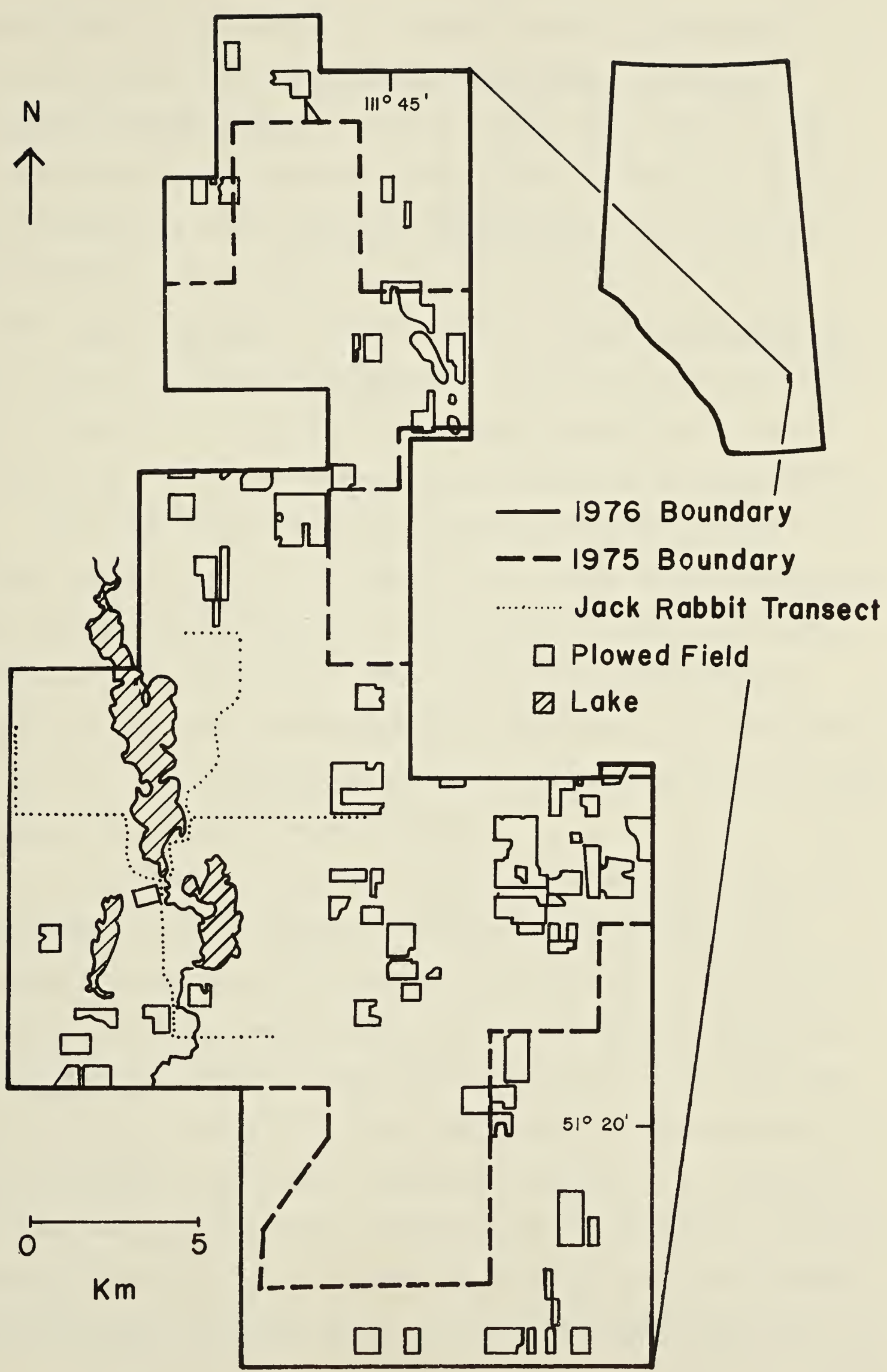
question by studying the overlap in their food, breeding seasons, occupied space and nest sites. By documenting these attributes I was able to evaluate the degree of ecological segregation and competition among these three species of Buteo.

MATERIALS AND METHODS

Field work was conducted on a study area in southeastern Alberta (51° 25' Lat., 111° 45' Long.) that encompassed 335 km² in 1975 and 480 km² in 1976 (Fig. 1). The summers in southeastern Alberta are typically short and warm; winters are long and cold. Throughout the year the maximum and minimum temperatures, recorded at the Brooks weather station (100 km south-southeast of the study area), were 35° C and -37° C, respectively, in 1975 and 34° C and -34° C, in 1976. Annual precipitation was 55 cm in 1975 and 34 cm in 1976.

The landscape is relatively level with gentle undulations. Elevation ranges from approximately 770-890 m. Valleys have been eroded by water, resulting in the formation of coulees. In addition to numerous man-made and natural ephemeral ponds in shallow depressions, there are also three man-made lakes covering 12 km². Settlement of the grasslands used for this study began in 1901 when the land was cultivated for grain production. Economic depression and drought during the 1930's resulted in farmers moving to other parts of the province (MacGregor 1975) and the land reverted again to grasslands. Grazing, where the dominant vegetation is grass (Gramineae), is now the common land use with only a limited amount of cultivation. In both years approximately 8% of the study area was used for grain

Figure 1. Study area with 1975 and 1976 boundries, location of lakes, cultivated fields and four routes of jack rabbit census.



production. Dense cover in certain areas is provided by shrubs: silver willow (Eleagnus commutata), snowberry (Symphoricarpos albus). Willows (Salix spp.) grow around permanent and semipermanent water bodies. Trees are sparse and consist of aspen (Populus tremuloides) growing around intermittent ponds and introduced varieties such as box elder (Acer negundo), Russian poplar (Populus petrowskyana) and caragana (Caragana arborescens) planted by man for shade and windbreaks. A list of vertebrates encountered on the study area during the summer period is given in Appendix 1.

In order to establish the timing of events in the annual cycle of the three species of hawks, I was present on the study area from April 11 to October 11, 1975 and from March 8 to September 20, 1976. During each season, the timing of arrival and departure of the hawks, the sequential events in their reproductive cycles and the locations of all their occupied nests were recorded.

To determine whether a surplus of mature individuals was present on the study area which were prevented from breeding by the territoriality of the resident population, territorial males were removed using a technique described by Hamerstrom (1963). This was done before or at the time of laying in 1976. Only males were removed because only they defended their nests vigorously enough to be caught. Females were never caught before the young hatched. The two ferruginous hawks captured were measured, banded and marked with patagial color-markers. A crescent-shaped piece of

herculite material was folded over the wing and held together by a "pop rivet" between secondary and tertiary feathers (Kochert in prep.). They were released on the day they were trapped: one approximately 100 km east of the study area and the other approximately 150 km southeast. It was hoped that, if they attempted to return, this distance would detain them long enough to allow any nonterritorial males present on the study area at that time to replace them. Three male Swainson's hawks, trapped in the same manner, were held in captivity until they had been replaced by other resident, but presumably previously nonterritorial, males.

Pairs nested closer to pairs of the other species than pairs of the same species in 1975, possibly because of differences in territorial aggressiveness. In order to detect such differences, captive ferruginous, Swainson's and red-tailed hawks were tethered to a low perch at a distance between 100 and 200 m from the nests of 11 ferruginous and 11 Swainson's hawks. The nest site was then approached until the incubating bird flushed and circled above the nest site. This presumably assured that at least one member of the pair would see the "intruder". The observer then withdrew and observed for 30 minutes from a distance of at least 0.7 km through binoculars or a telescope and recorded the nature and frequency of all interactions between resident birds and the tethered "intruder".

In order to minimize disturbance and the possibility of

desertion, nests were visited only shortly before the young were expected to hatch. A mirror fastened to the end of a telescoping fishing pole was used to examine nest contents and record clutch size before hatching. Hatching had occurred in some nests before the first visit. In these cases the clutch size was assumed to equal the number of young less than 1 week old plus any eggs still present in the nest at the time. If the young were older than 1 week when the nest was first visited no clutch size was recorded for that particular nest.

Food habits of these three species of hawks were based on pellets collected and prey items recorded at nests that were visited daily except on cold and rainy days. Visits were made at varying times of the day. The species, age and sex of all prey items were recorded when possible. Prey items were marked, by cutting off all legs, to avoid counting them twice yet leaving them as food for the nestlings. To prolong the period during which prey items could be recorded, two nestlings at the nest sites of 10 ferruginous and 7 Swainson's hawks were tethered on platforms (Peterson and Keir in press) for 2 to 15 days in 1975. Because there was only room for two nestlings on any one platform, any additional young had to be put into other nests of the same species to assure that the parents brought food to the tethered young. Weights of prey items used in the prey biomass calculations were based on weights of live individuals in the field and museum specimens (Appendix 2).

In 1976, four 8 mm movie cameras (Kodak Instamatic M4) were installed at nests of four ferruginous and one Swainson's hawk in order to estimate the total number and kinds of prey brought to the nests during the nestling stage. These cameras were contained in metal ammunition boxes with glass windows. A timing device (Miratronics Engineering, Edmonton; Model 315) was adjusted to expose one to five frames of film at a frequency of 2 to 4 minutes.

The abundance of potential prey was estimated. Voles (Microtus sp. and Lagurus curtatus) and mice (Peromyscus sp. and Zapus princeps) were estimated using 100 snaptraps set over a three-night period. Traps, placed in a straight line about 80 cm apart, were baited with peanut butter and set in runways when these could be recognized. They were set each evening and sprung the next morning and the numbers and kinds of rodents caught recorded. In 1975, 15 locations were sampled for a total of 4500 trap nights. In 1976, 10 locations were sampled for a total of 3000 trap nights. In choosing the sampling locations an attempt was made to sample in areas of different habitat. The abundance of white-tailed jack rabbits (Lepus townsendii) was estimated by counting the number seen on four different 8-km transects (Fig. 1) from 0.5 to 2 hours after sundown. This was done from a vehicle driving about 30 km per hour using a spotlight to search the roadsides. Counts were conducted once a week, a total of 14 times in 1975 and 17 times in 1976. Populations of ground squirrels were estimated by

first counting the number of occupied burrows on transects across six plots on which the density of ground squirrels was known. Burrows also were counted, while driving on a trailbike at slow speed, on transects across the grassland outside the plots. The density of ground squirrels on the study area was then extrapolated from the index achieved on the plots. Seventy transects, 0.7 km in length and radiating out from 21 hawk nests, were run in 1975 and 60 transects from 12 nests were run in 1976.

To determine if food brought to the nests was sufficient to permit the maximum rate of nestling growth, Richardson's ground squirrels (Spermophilus richardsonii) were added to nests in addition to the food brought by adults. The ground squirrels were shot on the study area and added to three nests of ferruginous hawks at the rate of 0.5 squirrels per nestling per day initially. This amount was gradually increased to 1.5 squirrels per nestling per day before fledging. Because of their smaller size nestling Swainson's hawks at three nests received 0.3 squirrels, increasing to 1.0 squirrel per nestling per day before fledging. Squirrels were added to nests from the time the nestlings were about 1 week old until they fledged. A total of 328 squirrels were added to nests of ferruginous hawks during periods of 32, 38 and 44 days. A total of 160 squirrels were added to nests of Swainson's hawks during periods of 24, 35 and 40 days.

The weights of nestling hawks in all nests on the study area were recorded to determine if their growth rates were related to the density of nesting hawks and to compare the rate of growth between augmented and unaugmented nests. The growth of right primary remex number four (Appendix 3) was measured as an index to estimate the hatching dates of nestlings (Hamerstrom unpublished). Some nestlings were measured only once, others at intervals of 3 to 8 days.

As an aid to estimating their home ranges, four breeding ferruginous and eight breeding Swainson's hawks were trapped (Hamerstrom 1963) after their nestlings were at least 2 weeks of age but before they fledged. These birds were color-marked using patagial markers as described above.

To compare the nest sites of the three species, the height above ground, the height of the tree, the area and depth of the nest and its exposure to the sun were measured. The type of nest material used was recorded also.

In autumn 1975, the number of available nesting sites was increased by erecting 93 poles with nest platforms attached (Appendix 4). This was done attempting to artificially increase the density of nesting hawks on a part of the study area.

RESULTS AND DISCUSSION

Natural History of the Hawks

Ferruginous Hawk

Ferruginous hawks are the largest of the North American buteos (Bent 1961). Two adult males trapped on the study area averaged 1422 g (1253-1590 g) and five adult females averaged 1854 g (1623-2030 g). This species nests in open dry country in the western United States and southwestern Canada (Fig. 2) and winters in northern Mexico and the southwestern United States (Bowles and Decker 1931, Brown and Amadon 1968). It was among the first hawks to arrive on the study area in spring, at about the same time as red-tailed but earlier than Swainson's hawks. This pattern of arrival among the three species was also observed on a study area in Utah (Smith and Murphy 1973). Ferruginous hawks nest in trees and on the ground (Cameron 1914, Bowles and Decker 1931, Godfrey 1966, Brown and Amadon 1968, Angell 1969, Smith and Murphy 1973, Howard and Wolfe 1976, Lokemoen and Duebbert 1976). The proportion of nests located on the ground varied from 2 to 52 % (Murphy et al. 1969, Howard and Wolfe 1976, Lokemoen and Duebbert 1976, this study). Ground nests are sometimes located on steep cliffs or cutbanks and even on hillsides (Bowles and Decker 1931, Lokemoen and Duebbert 1976, this study). Tree nests of this species range from 1.2 m to 14.6 m above ground (Bowles and Decker

Figure 2. Breeding ranges of three species of the genus Buteo (Salt 1939, Godfrey 1966, Brown and Amadon 1968).



1931, Woffinden 1975, Lokemoen and Duebbert 1976, this study). Sticks, primarily of sagebrush, sod, bark and bovid dung are most frequently used to build their nests but various other objects such as bones, paper and wire are often added (Bowles and Decker 1931, Angell 1969, Murphy et al. 1969, Lokemoen and Duebbert 1976, this study). The number of eggs laid varies from one to six, most often three or four (Angell 1969, Murphy et al. 1969, Smith and Murphy 1973, Lokemoen and Duebbert 1976, this study). Different incubation periods have been reported; 25 days (Cameron 1914), 28 days (Brown and Amadon 1968). These periods are probably minimal based on data in Smith and Murphy (1973) who reported mean laying and hatching dates for 4 consecutive years. I calculated a mean incubation of 36 days from their data. Average hatching dates for this hawk in Utah varied between May 10 and 12 over four years (Smith and Murphy 1973) and between May 27 and June 4 in the two years of this study. The average nestling period was about 46 days (Angell 1969, this study). After fledging ferruginous hawks appear to remain for several weeks near their own nest sites in family groups (this study). A color-marked individual was last seen about 1 km from its nest site on August 10, 1976, 29 days after the young fledged. A dark phase adult was still present near its nest on August 21, 1976, 53 days after the young fledged.

Prey items of this species include members of
Lagomorpha, Rodentia, Carnivora, Anseriformes,

Charadriiformes, Galliformes, Passeriformes, Squamata, and Orthoptera (Cameron 1914, Gloyd 1925, Bowles and Decker 1931, Brown and Amadon 1968, Angell 1969, Murphy et al. 1969, Smith and Murphy 1973, Howard and Wolfe 1976, Lokemoen and Duebbert 1976, this study). Those prey species which have been reported to comprise more than 30% of prey biomass were: black-tailed jack rabbits (Lepus californicus) in Utah (Murphy et al. 1969, Smith and Murphy 1973, Howard and Wolfe 1976), Ord's kangaroo rats (Dipodomys ordii) in Utah (Murphy et al. 1969) and Richardson's ground squirrels in South Dakota (Lokemoen and Duebbert 1976) and Alberta (this study).

Swainson's Hawk

Swainson's hawks are much smaller in body weight than ferruginous hawks. Forty-two adult male Swainson's hawks trapped on the study area averaged 804 g (683-886 g) and 29 adult females averaged 1111 g (938-1234 g). This species breeds in western North America (Fig. 2) and winters mainly in Argentina with some individuals in Florida (Brown and Amadon 1968). This hawk typically nests only in shrubs or trees which were of various heights (Godfrey 1966, Brown and Amadon 1968, Dunkle 1977, this study). The height of the nest above ground may vary from 0.8 m to 30 m (Brown and Amadon 1968, Dunkle 1977, this study). Nests are built of sticks and lined with leafy twigs, bark, forbs and grasses (Brown and Amadon 1968, Dunkle 1977, this study). The

number of eggs laid varies from one to four, most frequently two or three (Godfrey 1966, Brown and Amadon 1968, this study). The incubation period is 28 days (Godfrey 1966, Brown and Amadon 1968, this study). Eggs hatched in Utah on May 21, 27, June 6, 11, and 16 in five nests over 4 years (Smith and Murphy 1973). In Wyoming eggs hatched between May 16 and July 3 in one year (Craighead and Craighead 1969) and in Alberta, hatching occurred between June 15 and July 17 in two years (this study). The nestling period was about 42 days (Craighead and Craighead 1969, this study). After fledging Swainson's hawks also seem to remain in the vicinity of the nest site. The last observation of a color-marked adult was about 0.5 km from its nest site on September 17, 1976, 39 days after its young fledged.

Prey items of this species include members of Chiroptera, Lagomorpha, Rodentia, Carnivora, Anseriformes, Galliformes, Charadriiformes, Passeriformes, Squamata, Amphibia, Pisces and Insecta (Cameron 1914, Gloyd 1925, Bowles and Decker 1934, White 1966, Brown and Amadon 1968, Littlefield 1973, Smith and Murphy 1973, Dunkle 1977, this study). The prey items comprising 30% or more of prey biomass were: black-tailed jack rabbits in Utah (Smith and Murphy 1973), Uinta ground squirrels (Spermophilus armatus) in Wyoming (Craighead and Craighead 1969) and Richardson's ground squirrels in Alberta (this study). There are many accounts of this hawk feeding on insects outside the nestling period suggesting that this may be an important

prey item at this time (Cameron 1914, Gloyd 1925, Bowles and Decker 1931, White 1966, Brown and Amadon 1968, Littlefield 1973).

Red-tailed hawk

Red-tailed hawks are intermediate in weight between Swainson's and ferruginous hawks. Average weights of males and females are 1028 g and 1224 g, respectively, (Brown and Amadon 1968). These hawks breed throughout North and Central America where suitable nest sites are available (Fig. 2) and winter in the southern parts of their range (Brown and Amadon 1968). Their nests, found on trees, cacti and cliffs (Fitch et al. 1946, Brown and Amadon 1968, Smith and Murphy 1973, this study), are made of sticks, lined with leafy twigs and bark (Brown and Amadon 1968, this study). Nests vary in height above ground from 4 to 21 m (Fitch et al. 1946, Brown and Amadon 1968, this study). One to four eggs are laid, usually three, and incubation lasts between 28 and 32 days (Fitch et al. 1946, Brown and Amadon 1968, Smith and Murphy 1973). Eggs hatched between April 17 and May 14 in Utah over a period of 4 years (Smith and Murphy 1973), between May 14 and 27 in Wyoming (Craighead and Craighead 1969) and in Alberta between June 1 and 16 over a period of 6 years (McInville and Keith 1974) and between June 2 and 4 during the two years of this study. Nestlings remained in the nests 41 (Craighead and Craighead 1969) and 46 days (Fitch et al. 1946). Family groups were observed in

California up to 92 days after fledging (Fitch et al. 1946).

Prey items of this hawk, in those parts of their range where they may be potentially sympatric with ferruginous or Swainson's hawks, include members of Insectivora, Lagomorpha, Rodentia, Anseriformes, Falconiformes, Galliformes, Charadriiformes, Passeriformes, Serpentes and Amphibia (Fitch et al. 1946, Luttich et al. 1969, Tyler and Saetveit 1969, Smith and Murphy 1973). Those prey items which comprised 30% or more of the total biomass were: California ground squirrels (Spermophilus beecheyi) in California (Fitch et al. 1946), black-tailed jack rabbits in Utah (Smith and Murphy 1973), snowshoe hares (Lepus americanus) (McInville and Keith 1974) and Richardson's ground squirrels (Luttich et al. 1970, McInville and Keith 1974, this study) in Alberta.

Food Resource Overlap

Food is the most critical resource for most birds (Baker and Baker 1973) in terms of survival and successful reproduction. Coexisting species may segregate themselves ecologically by using different food resources (Gibb 1954, Lack 1971, Cody 1974). This is achieved by using different kinds of food in the same area, by using different hunting methods to take different portions of a given food source or by feeding on a common food source at different times or in different places.

Food habits

The food habits of raptors are most easily studied during the nesting season when food and pellets can be found at the nest. Although prey density often tends to be greatest during the summer period, because of prey reproduction, hawks may be forced to nest in aggregations of higher densities in available habitat suitable for nesting (Newton 1976). This is particularly true in prairie habitat where nest sites may be scarce, forcing closely associated pairs to share the food (Rand 1952). Therefore, closely related species nesting in the same habitat may be expected to exhibit differences in their food habits to reduce competition.

The food habits of raptors can be studied by analyzing either pellets or prey species found at nests. Each of these methods can potentially bias the results. Pellets are cast by hawks about 20 hours after eating (Duke et al. 1975). Adult hawks usually, but not always, cast a pellet after each meal (Duke et al. 1975). Pellets are a potentially inaccurate indicator of food habits for several reasons. For example, nestlings may feed on the same prey item for 2 days, producing one pellet each day which contains the remnants of the same prey item. Consequently, use of these pellets to estimate prey consumed would overestimate the number (Glading et al. 1943). On the other hand, often only the fleshy parts of large prey items such as ground squirrels and jack rabbits are eaten. Under these

circumstances few pellets are produced and the number of these items in the diet would be underestimated (Glading et al. 1943). Of nine kangaroo rats fed to a Swainson's hawk, only three were evident in its pellets (Glading et al. 1943) and of 17 amphibians fed to a rough-legged buzzard (B. lagopus lagopus Bruenn.) none were evident in its pellets (Pasanen and Sulkava 1971). Glading et al. (1943) also suggested that down feathers and soft bones, such as in young prey items, are not regurgitated in pellets but pass directly through the digestive tract. The importance of rarer items could be overestimated by pellet analysis since it is impossible to determine the number of prey items represented in pellets. Pellets are very useful indicators of food habits of owls, which do not digest all bones, but are only of limited value in the study of food habits of hawks which digest bones almost entirely (Errington 1932, Glading et al. 1943, Pasanen and Sulkava 1971).

The use of prey items alone as a record of prey taken, probably overestimates larger prey because parts of such prey may still be present in the nest after one or several meals whereas small prey are often devoured whole (Fitch et al. 1946, Pasanen and Sulkava 1971). However, it is also possible that larger items are eaten before smaller items because larger items are more obvious and may attract a nestling more often than smaller items (Fitch et al. 1946). In two instances, in nests monitored photographically by movie cameras, a ground squirrel was fed to the young by the

adult hawk before a mouse that was present in the nest at the same time.

The number of nests and the frequency at which these were visited is shown in Table 1. In 1975, 344 pellets were collected on 1115 visits. A large number of pellets must have gone unnoticed; some crumble after drying and become mixed with nest material (Glading et al. 1943) and others may have been blown from the nest by the wind. Young nestlings probably do not regurgitate pellets (Pasanen and Sulkava 1971). These factors are probably responsible for the lower number of pellets observed than expected during 1115 visits. An attempt was made to collect all pellets in 1975. In 1976, only 108 pellets were collected because I had hoped that the use of time-lapse cameras would provide a more exact means of correcting errors in prey analysis based on prey items. This hope was not fulfilled and therefore I estimated the proportion of prey items taken by using the evidence of prey found in pellets plus prey items recorded on daily visits to the nests. The methods are complimentary because prey recorded in the nest tends to be biased toward larger items whereas prey recorded from pellets tends to be biased toward the smaller items (Fitch et al. 1946). This procedure was used to document the food habits of ferruginous, Swainson's, and red-tailed hawks during this study. Assuming that on day "x" a ground squirrel was found in the nest and on day "x+1" three pellets were found in a nest which had three nestlings. Each pellet contained

Table 1. Number of times the nests of hawks were visited for prey analysis.

	Number of Nests		Number of Visits		Mean Number of Visits per nest	
	1975	1976	1975	1976	1975	1976
Ferruginous Hawk	26	24	527	493	20	21
Swainson's Hawk	24	39	512	460	21	12
Red-tailed Hawk	3	1	63	35	31	35

ground squirrel hair and one contained mouse hair. It was then assumed that on day "x" one ground squirrel and one mouse were eaten. It is possible that two or even three ground squirrels were eaten but this is impossible to determine. Hair in pellets was identified by length and color pattern as that of ground squirrel, mouse or jack rabbit. Avian prey remains in pellets could not be classified beyond the class Aves. The prey summary represents the prey brought by adults to their young during the nestling stage. The extent to which this also represents the food habits of adults is not known. Adult hawks were observed eating ground squirrels near their nest sites, suggesting that their diet is probably similar to that of their nestlings.

All three species relied primarily on Richardson's ground squirrels as their prey (Tables 2, 3, and 4). Red-tailed hawks (Table 4) appeared to have a diet similar to ferruginous (Table 2) and Swainson's hawks (Table 3) but the number of nests at which prey was recorded, three in 1975 and one in 1976, was too small for a valid comparison of this sample with the much larger sample for the other two species. The low number and restricted distribution of nesting red-tailed hawks on the study area itself suggests a tendency to occupy different habitat than ferruginous hawks. Thus, these two species were only narrowly sympatric in this area (see Habitat section).

Table 2. Prey of ferruginous hawks based on carcasses and pellets found in the nests during the nestling period.

	Total Numbers		% of Items		% of Biomass	
	1975	1976	1975	1976	1975	1976
Ground squirrels ¹	538	554	86.1	92.3	89.4	88.8
(<u>S. richardsonii</u>) ²	486	548				
(<u>S. tridecem-</u> <u>lineatus</u>) ²	1	0				
Voles and mice ¹	35	7	5.6	1.2	0.7	0.1
(<u>Microtus</u> sp.) ²	8	2				
(<u>L. curtatus</u>) ²	1	0				
(<u>Peromyscus</u> sp.) ²	1	2				
(<u>Z. princeps</u>) ²	1	0				
Jack rabbits ¹	6	16	1.0	2.7	3.5	9.1
(<u>L. townsendii</u>) ²	4	15				
Birds ¹	46	23	7.4	3.8	6.4	1.9
Anseriformes ²	8	4				
Galliformes ²	0	1				
Charadriiformes ²	0	1				
Passeriformes ²	19	13				

¹ Based on carcasses and pellets combined.

² Based on carcasses alone.

Table 3. Prey of Swainson's hawks based on carcasses and pellets found in nests during the nestling period.

	Total Numbers		% of Items		% of Biomass	
	1975	1976	1975	1976	1975	1976
Ground squirrels ¹	422	255	67.7	71.2	81.7	69.1
(<u>S. richardsonii</u>) ²	369	238				
(<u>S. tridecem-</u> <u>lineatus</u>) ²	2	4				
Voles and mice ¹	84	42	13.5	11.7	1.6	1.1
(<u>Microtus</u> sp.) ²	46	18				
(<u>L. curtatus</u>) ²	0	2				
(<u>Peromyscus</u> sp.) ²	1	7				
 (<u>Ondatra</u> <u>zibethicus</u>) ²	 0	 2	 0	 0.6	 0	 1.6
Jack rabbits ¹	3	10	0.5	2.8	4.6	21.7
(<u>L. townsendii</u>) ²	3	8				
 (<u>Mustela erminea</u>) ²	 0	 1	 0	 0.3	 0	 0.1
Birds ¹	114	40	18.3	11.2	12.1	6.1
Anseriformes ²	38	12				
Galliformes ²	4	3				
Charadriiformes ²	13	7				
Passeriformes ²	23	10				
 (<u>Thamnophis</u> spp.) ²	 0	 5	 0	 1.4	 0	 0.4
 (<u>Ambystoma</u> <u>tigrinum</u>) ²	 0	 1	 0	 0.3	 0	 <0.1
 Insects ¹	 2	 2	 0.1	 0.5	 <0.1	 <0.1

¹ Based on carcasses and pellets combined.

² Based on carcasses alone.

Table 4. Prey of red-tailed hawks based on carcasses and pellets found in nests during the nestling period.

	Total Numbers		% of Items		% of Biomass	
	1975	1976	1975	1976	1975	1976
Ground squirrels ¹	39	23	48.2	74.2	63.3	89.5
(<u>S. richardsonii</u>) ²	36	23				
Voles, mice and shrews ¹	7	0	8.6	0	1.4	0
(<u>Microtus</u> sp.) ²	6	0				
(<u>Sorex</u> spp.) ²	1	0				
Birds ¹	35	0	43.2	25.8	35.3	10.5
Anseriformes ²	16	2				
Passeriformes ²	13	6				

¹ Based on carcasses and pellets combined in 1975, on carcasses alone in 1976.

² Based on carcasses alone.

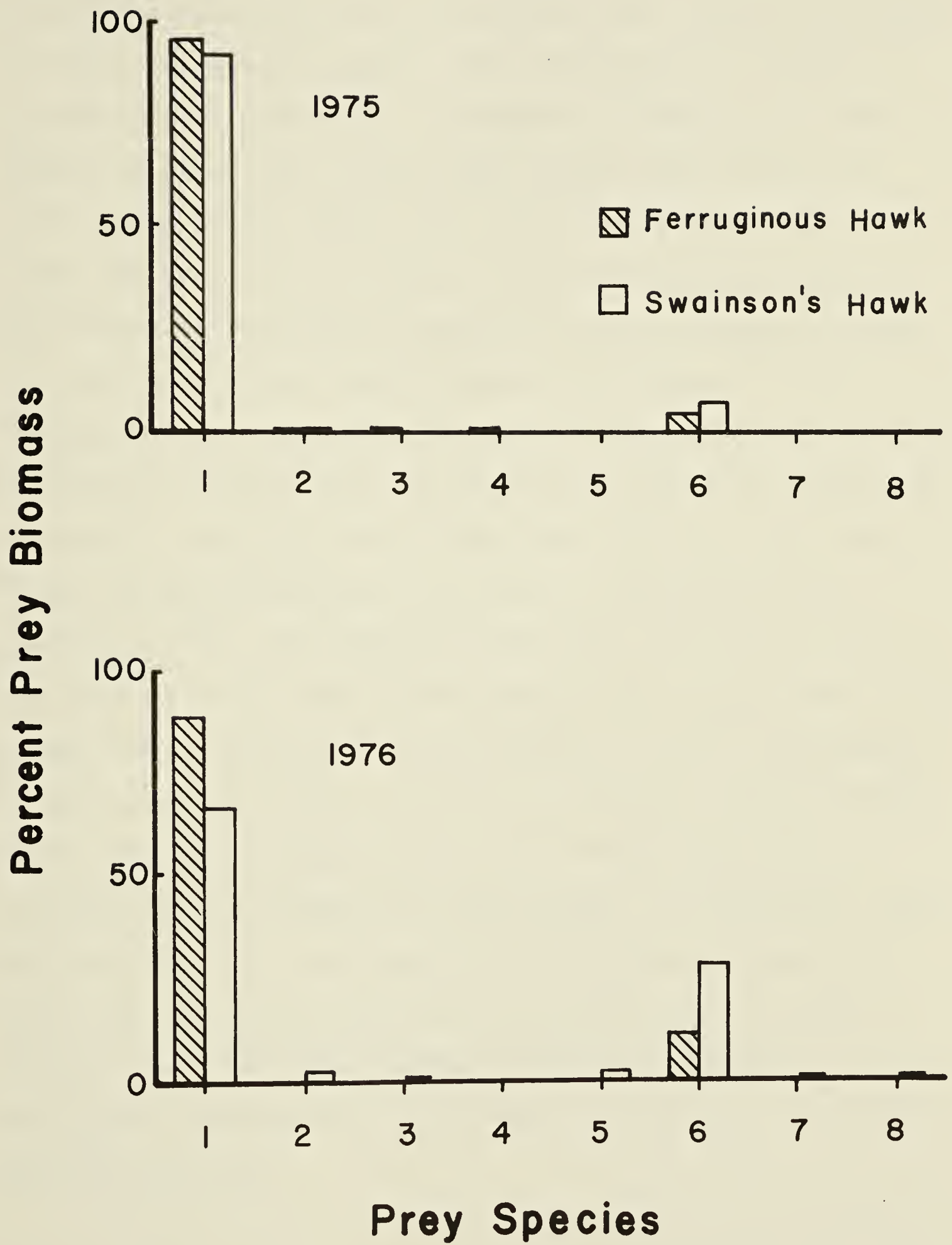
A prey species is considered important if it comprised at least 5% of the total diet (Schoener 1965). Of all prey items recorded from nests of ferruginous and Swainson's hawks in 1975, 93% and 75% respectively, were identified at the species level and in 1976, 96% and 80% respectively. In terms of biomass of the prey identified at the species level, the important prey species in 1975 were Richardson's ground squirrels for ferruginous hawks and Richardson's ground squirrels and jack rabbits for Swainson's hawks. In 1976 Richardson's ground squirrels and jack rabbits comprised more than 5% of the prey biomass of both ferruginous hawks and Swainson's hawks. With the exception of jack rabbits in 1975, therefore, the same categories of prey are important to both species. Although the two species took the same kinds of prey, the proportions in each category differed. I tested the relative percent biomass of the important prey categories taken by ferruginous and Swainson's hawks for equality of percentages (Sokal and Rohlf 1969) and found no significant differences in 1975. In 1976 however, the proportion of jack rabbits taken by the two species was not significantly different but ferruginous hawks took a significantly greater proportion of Richardson's ground squirrels ($P < 0.05$) than Swainson's hawks. I calculated the total dietary overlap between these hawks by summing the percentages of each of the prey species that were common to both species of hawks (Holmes and Pitelka 1968). If, for example, prey species "a" formed 70%

of the diet of hawk species "1" and 50% of the diet of hawk species "2", the percentage in common to the diet of both species of hawks was 50. These common percentages were summed for all prey species and the resulting value represents a measure of the degree to which ferruginous and Swainson's hawks overlapped in their use of the food resource. The total dietary overlap, based on prey items, was 99% and 95% in 1975 and 1976, respectively. Based on prey biomass, the total dietary overlap was 98% in 1975 and 82% in 1976 (Fig. 3). A similar overlap in the diet of ferruginous and Swainson's hawks has been reported by Smith and Murphy (1973). From their data I calculated the dietary overlap based on numbers of prey items in each of two years as 61 and 37% and in prey biomass as 98 and 84%. The food overlap of four species of eagles in eastern Africa varied from 21 to 66% based on numbers of prey and from 40 to 78% based on biomass of prey (Smeenk 1974). It is difficult to determine the point at which dietary overlap reflects ecological segregation relative to the food resource. A dietary overlap of 82% or 98% is very high and one would expect these species to be segregated in ways other than by taking different kinds of food.

Body Size

It has been shown that hawks of different sizes or weights tend to partition their food resource on the basis of prey weight (Schoener 1965, Storer 1966, van Beusekom

Figure 3. Dietary overlap between ferruginous and Swainson's hawks, based on prey items identified to species: (1) Spermophilus richardsonii, (2) S. tridecemlineatus, (3) Lagurus curtatus, (4) Zapus princeps, (5) Ondatra zibethicus, (6) Lepus townsendii, (7) Mustela erminea, and (8) Ambystoma tigrinum.



1972, Reynolds 1972, Smith and Murphy 1973). Adult Swainson's hawks are, on the average, only 59% of the weight of adult ferruginous hawks. This difference in weight is apparently not sufficient to produce a difference in the weight of prey taken, since both species took large and small prey. Jack rabbits were the largest prey taken by these two hawks. Of 35 jack rabbits recorded as prey, 22 were taken by ferruginous hawks and 13 by Swainson's hawks. As a measure of prey age and size, the hind foot of 12 individuals was measured. The mean length of those taken by ferruginous hawks was 80 mm (60, 60, 79, 85, 95, 103) and by Swainson's hawks was 107 mm (87, 100, 100, 107, 112, 138). Since the mean length of hind feet of adults is 150 mm (Banfield 1974), ferruginous hawks took individuals about one half of adult size and Swainson's hawks about two thirds adult size. Swainson's hawks preyed on larger individuals than ferruginous hawks, probably because the former nested later when jack rabbits were older. Thus, there was no evidence in this study that ferruginous and Swainson's hawks partitioned their food resource on the basis of prey size. Since the food habits of both ferruginous and Swainson's hawks on the study area appear to be very similar, ecological segregation on the basis of different prey taken must be ruled out.

Hunting Methods

Coexisting species may be ecologically segregated by exhibiting different hunting methods while feeding on the same resource and thereby are able to coexist (Kruuk 1967, Reynoldson 1975). Species of birds sometimes exhibit differences in their feeding methods that presumably result in different components of the food taken (MacArthur 1958, Lack 1971, Cody 1974). Most raptorial birds that take their prey from the ground hunt from a perch (Brown and Amadon 1968). Wakeley (1974) has described the hunting methods of ferruginous hawks on a study area where Townsend's ground squirrels (Spermophilus townsendii) and northern pocket gophers (Thomomys talpoides) were the largest available prey. He described ferruginous hawks hunting from the ground, from a perch, and in flight at both high and low altitudes. Most low altitude flight was below 20 m and most high altitude flight was above 100 m. Ferruginous hawks on the study area were also observed in low, fast flight, with rapid wingbeats, between approximately 1 and 7 m from the ground. By contrast, Swainson's hawks were rarely observed to fly low over the ground at high speed in the manner of ferruginous hawks. Low fast flight and hunting from the ground is only possible in open habitat and appears to be typical of ferruginous hawks.

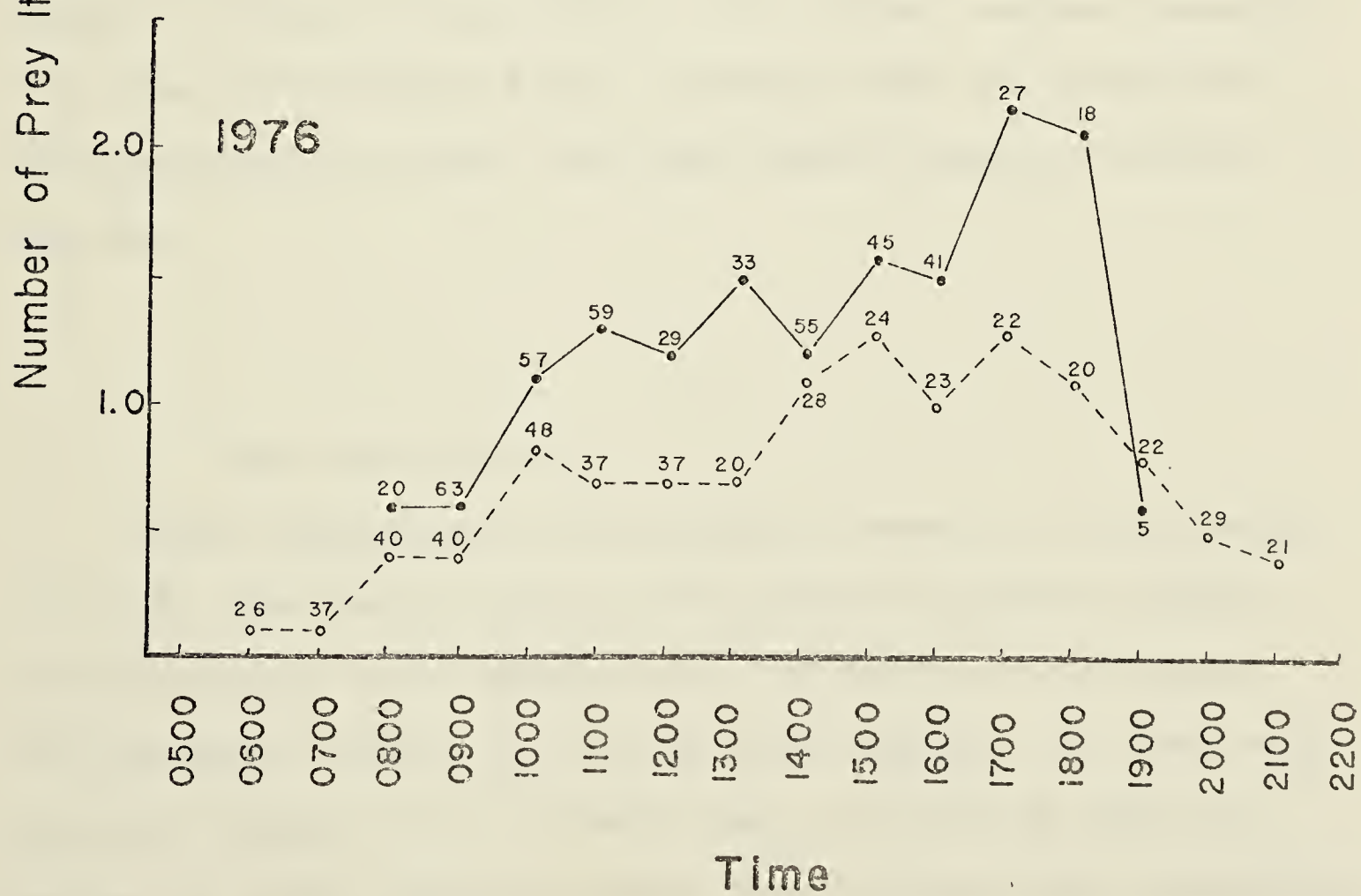
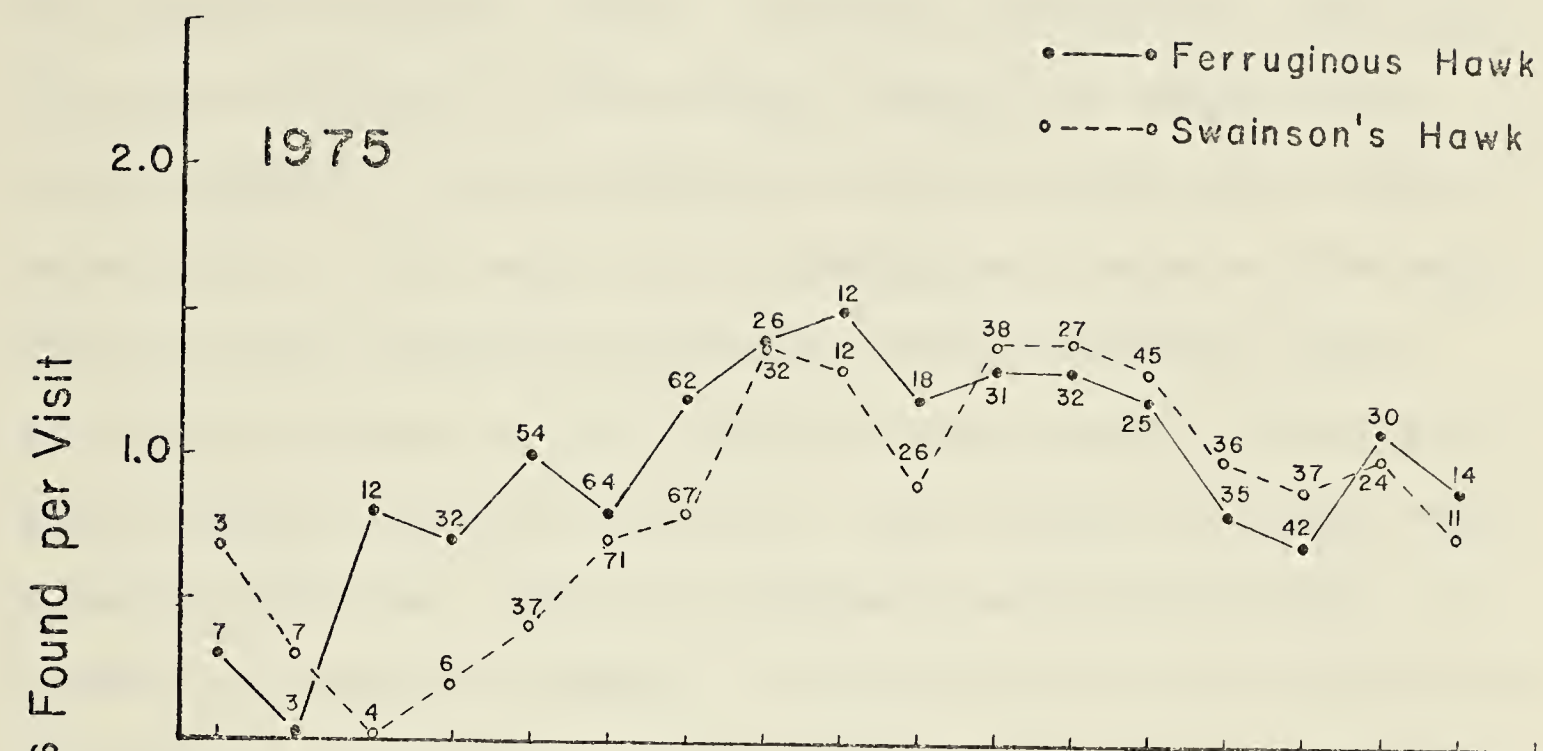
Although there appear to be differences in the hunting methods exhibited by ferruginous hawks and Swainson's hawks, it is doubtful that either method would select for a segment

of the populations of their main prey that was invulnerable to the other species. This supposition is supported by the fact that no significant difference ($G=1.35$) was found in the distribution of sex and age classes of Richardson's ground squirrels preyed upon by ferruginous and Swainson's hawks in July, both years included.

Hunting Times

Smith and Murphy (1973) have suggested that ferruginous hawks hunt from 0600 to 0900 hours and from 1800 to 2100 hours whereas Swainson's hawks hunt from 0900 to 1300 hours and from 1600 to 1900. According to Cody (1974), species using similar resources may coexist if they exhibit displacement in their hunting activity such as hawks and owls. If such displacement were occurring between ferruginous and Swainson's hawks, I predicted that the number of prey remains found in the nests of these two species also would show a displacement in time. In Fig. 4 the numbers of prey items found in nests of ferruginous and Swainson's hawks are shown throughout the day. It was impossible to determine the time at which a particular prey item was brought to the nest. However, it appears that prey items were brought to the nest throughout the day because no notable decline in the number of items found was apparent at any given time throughout the day. The data suggest that hunting activity may have been concentrated just before 1300, 1600 and 2000 hours. However, if this was so these

Figure 4. Number of prey items recorded in the nests of ferruginous and Swainson's hawks at various times throughout the day. Numbers above each point represent the number of visits.



hunting peaks were exhibited by both species alike. In Idaho ferruginous hawks hunted from 0600 to 1100 hours and from 1500 to 2000 hours with a reduced hunting activity in the interim (Wakeley 1974). Although ferruginous hawks may be active earlier in the morning (Smith and Murphy 1973) there appears to be no difference in the times prey items were found at the nest and by assumption, taken to the nest. This strongly supports Wakeley's (1974) contention that ferruginous hawks do not restrict their hunting activity to early morning and late evening. Even if hunting times were clearly different, only the frequency of interspecific encounters would be reduced. Competition for food would not be reduced because any item of prey removed by one species would no longer be available to the other, whether taken at the same or different times, assuming that the particular prey species was active over the hunting periods of both species.

Food Availability

Since ferruginous and Swainson's hawks overlap greatly in their food habits and do not appear to exhibit obvious differences by which competition for food may be reduced, the question arises, is food in short supply. If food were in short supply it is probable that the rate of gain in weight by young would be slower than if food were abundantly available to the nestlings (Ricklefs 1968). In order to

test this hypothesis, Richardson's ground squirrels, in addition to those brought to the nests by adult hawks, were added to nests of both ferruginous and Swainson's hawks and the growth rates of nestlings in these nests were compared to those in nests where such additions were not made.

Before the results of this experiment can be considered one must know first whether the addition of food actually resulted in more food available to the nestlings. Adults may have compensated for the added food by hunting only when their young were hungry (von Haartman 1953). I compared the mean number of all prey items found, those added plus those brought by adults, in experimental and control nests (Table 5). Only those nests visited more than 25 times were included in this comparison. The proportion of prey items found per visit was greater in nests where food was added than in control nests. This difference is not statistically significant for ferruginous hawks ($\chi^2=1.05$) but is highly significant for Swainson's hawks ($\chi^2=14.49$, $P<0.01$). The percent of times no prey was found in experimental nests was less than in control nests but this again was not statistically significant for ferruginous hawks ($\chi^2=2.03$) but was highly significant for Swainson's hawks ($\chi^2=9.07$, $P<0.01$). Thus, the addition of food resulted in more food available to the young although the difference was not significantly greater than in control nests for ferruginous hawks. Thus, these hawks may have compensated for the added food by reducing their hunting activity.

Table 5. Number of prey items present in hawk nests at each visit.

Number	Ferruginous Hawk		Swainson's Hawk	
	Prey Added	Prey Not Added	Prey Added	Prey Not Added
Visits	115	335	97	250
Without prey	39 (34%)	143 (43%)	40 (41%)	148 (59%)
With prey	76 (66%)	192 (57%)	57 (59%)	102 (41%)
Prey items	162	383	117	158
Mean number of items per visit	1.41	1.14	1.09	0.63

I compared slopes (Steel and Torrie 1960) of weight gained over time by both groups of nestlings (Fig. 5). Only the straight line portion of the growth curve was used in the statistical comparison (Hunt and Hunt 1975). This comparison yielded no significant difference between the slopes of these lines for the experimental and control groups (ferruginous hawks $t=0.061$, Swainson's hawks $t=0.043$). This suggests that food was sufficiently available to both ferruginous and Swainson's hawks to permit maximum rates of weight gain by their nestlings without the added food. These results also accord with observations of uneaten prey in the nests. Ground squirrels were readily available to the hawks judging by the number sometimes present in one nest. In one instance 16 ground squirrels were brought to a nest in one day.

In an attempt to provide further evidence that food was sufficiently abundant to absolve the hawks of any need to compete for it I estimated that portion of the Richardson's ground squirrel population being consumed by the nesting buteos. The average density of Richardson's ground squirrels was extrapolated for the whole study area from counts of ground squirrel burrows showing signs of habitation on plots of known density (Table 6). Counts of occupied burrows were carried out by a different person each year. This accounts for the difference in the absolute number of burrows counted. However, since the actual estimation is based on a comparison of the ratio of burrows

Figure 5. Comparison of the rate of body weight increase between nestlings with augmented and unaugmented food supply in 1976. The broken vertical line represents the mean date at which addition of food was initiated.

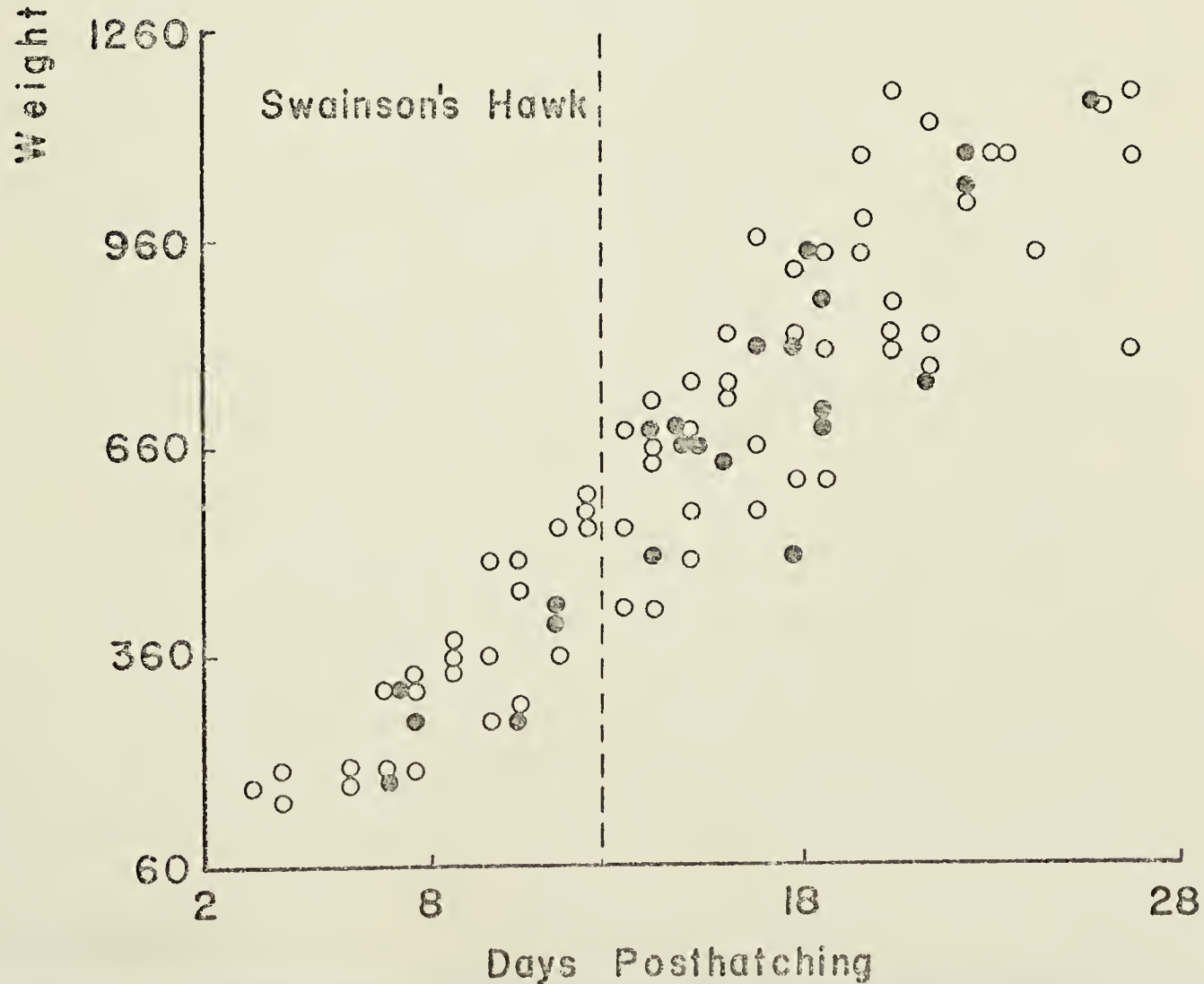
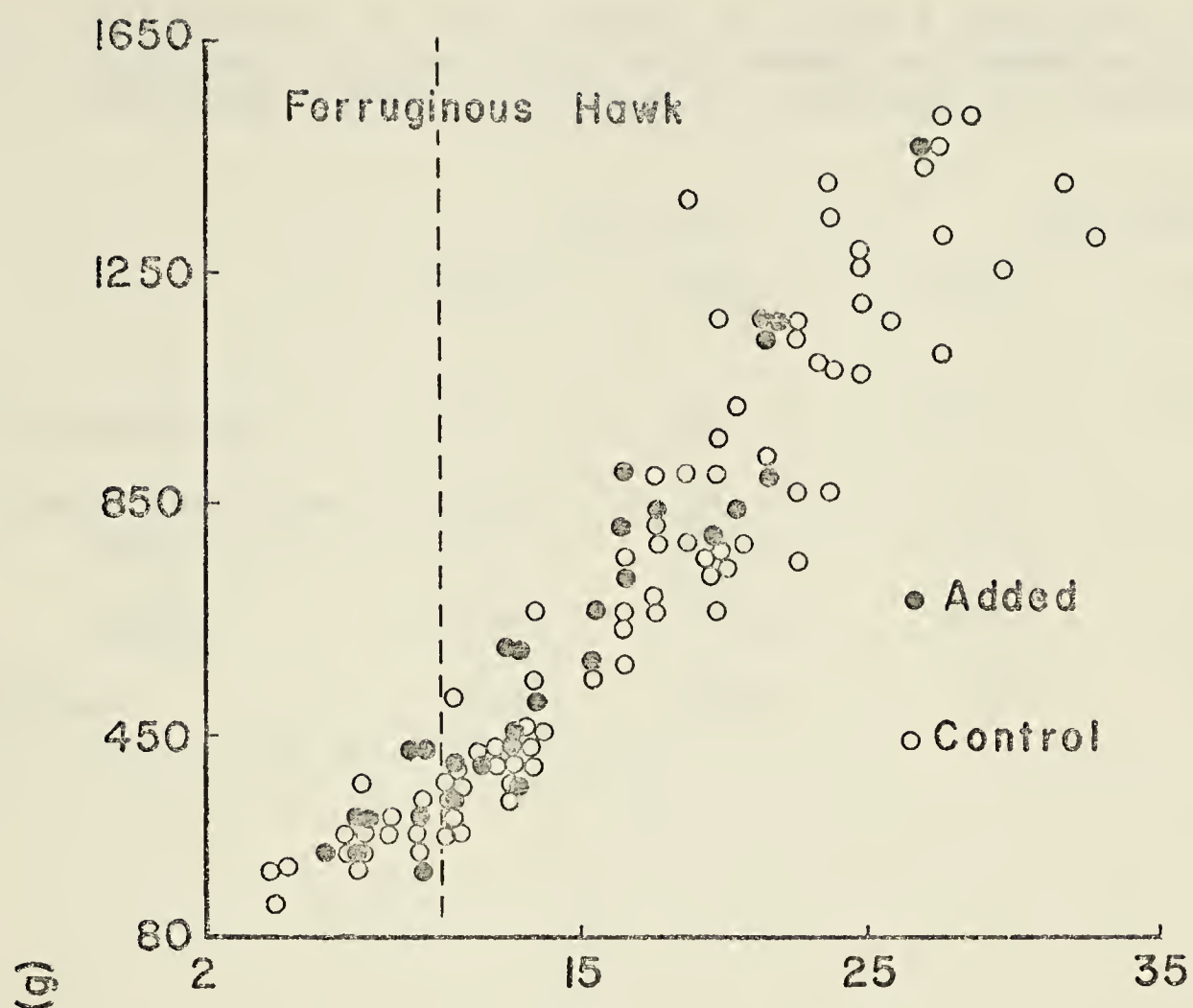


Table 6. Estimation of the density of ground squirrels (per hectare) on the study area based on numbers of occupied burrows counted on a series of transects.

	On Plot		Off Plot	
	1975	1976	1975	1976
No. of Transects	23	30	70	60
No. of Burrows/0.7km				
Mean	11.5	39.4	3.5	19.8
Range	2-27	11-84	0-13	0-83
Density/ha ¹	17.5	18.9	5.3	9.5

$$\text{Density/ha} = \frac{\text{squirrels/ha on plots} \times \text{burrows off plots}}{\text{burrows on plots}}$$

counted on and off the plots this method is valid as an index from which an interyear comparison can be made. This method assumes that the number of burrows in a given area is proportional to the number of ground squirrels in that area (Brown and Roy 1943).

The percent of the total Richardson's ground squirrel population taken by nesting buteos was calculated using the following equation:

$$\% = \frac{\text{dfr} \times \text{nb} \times 1.25 \times \text{pd} \times \text{t} \times 100}{\text{wt} \times \text{ngs}}$$

where:

dfr = daily food requirement of hawks in grams

nb = number of buteos

1.25 = wastage (Brown and Amadon 1968)

pd = proportion of diet comprised of Richardson's
ground squirrels

t = number of days hawks were present on the study
area

wt = mean weight in grams of adult and juvenile
Richardson's ground squirrels based on
proportions of these in the hawks' diet during
the nestling stage and on proportions in the
live population outside the nestling stage

ngs = number of Richardson's ground squirrels on the
study area

Food requirements of nestlings of the three species are reported by Olendorff (1973). Daily food requirements of adult buteos were based on a pair of captive ferruginous hawks during this study and captive red-tailed hawks (Craighead and Craighead 1969), they were extrapolated for Swainson's hawks using data for ferruginous and red-tailed hawks. The proportion of Richardson's ground squirrels in the total prey was based on data from Tables 2, 3 and 4 and the number of days adults were present on the study area was based on Fig. 3. The daily food requirements of young buteos after fledging were assumed to equal those of adults. The proportion of Richardson's ground squirrels in the prey was assumed to remain the same before and after the nestling period. Pairs associated with unsuccessful nests were presumed to have left the study area after June.

According to these estimations, nesting buteos on the study area removed 15% of the total Richardson's ground squirrel population in 1975 and 6% in 1976. The smaller percentage in 1976 probably does not reflect the observed decrease of Richardson's ground squirrels in the hawks' diets alone (Tables 2, 3 and 4) but rather the increase in the estimated density of Richardson's ground squirrels from 5.3 to 9.5 per ha. This increase may represent an overestimate since populations of Richardson's ground squirrels on plots of known density rose only from 17.5 to 18.5 per ha. Nevertheless, the percentage of the total population of Richardson's ground squirrels preyed upon was

probably less than 15%. This is much less than observed annual mortality in these squirrels (S. Schmutz 1977) and this prey was sufficiently abundant to make it an unlikely factor limiting the breeding population of buteos.

According to Lack (1946, 1971), species of birds, normally segregated by food niche, may overlap greatly in their diet and still coexist when food is temporarily superabundant. Holmes and Pitelka (1968) found that the overlap in food of sandpipers was higher in those seasons when food was more abundant. In order to determine whether Richardson's ground squirrels on the study area were temporarily superabundant, I compared the estimates of population density on the study area with those reported for other areas (Table 7). It appears that the population levels of Richardson's ground squirrels during the 2 years of this study were not abnormally high, but probably within the normal range of population fluctuation for this species. It is unlikely therefore, that the extensive overlap in food habits is merely a result of temporary superabundance of prey.

Table 7. Estimates of the density of populations of Richardson's ground squirrels.

Location	Density estimate	Authority
Highmore, South Dakota	6-8 squirrels/ha	Gunderson (1961)
Kayville, Sask.	0.9-1.4 adults/ha	Michener and Michener (1977)
Rochester, Alta.	0.7-19.5 adult females/ha	Dorrance (1974)
Hanna, Alta.	3.3-7.0 adult 3.8-7.5 adult females/ha	S. Schmutz (1977)

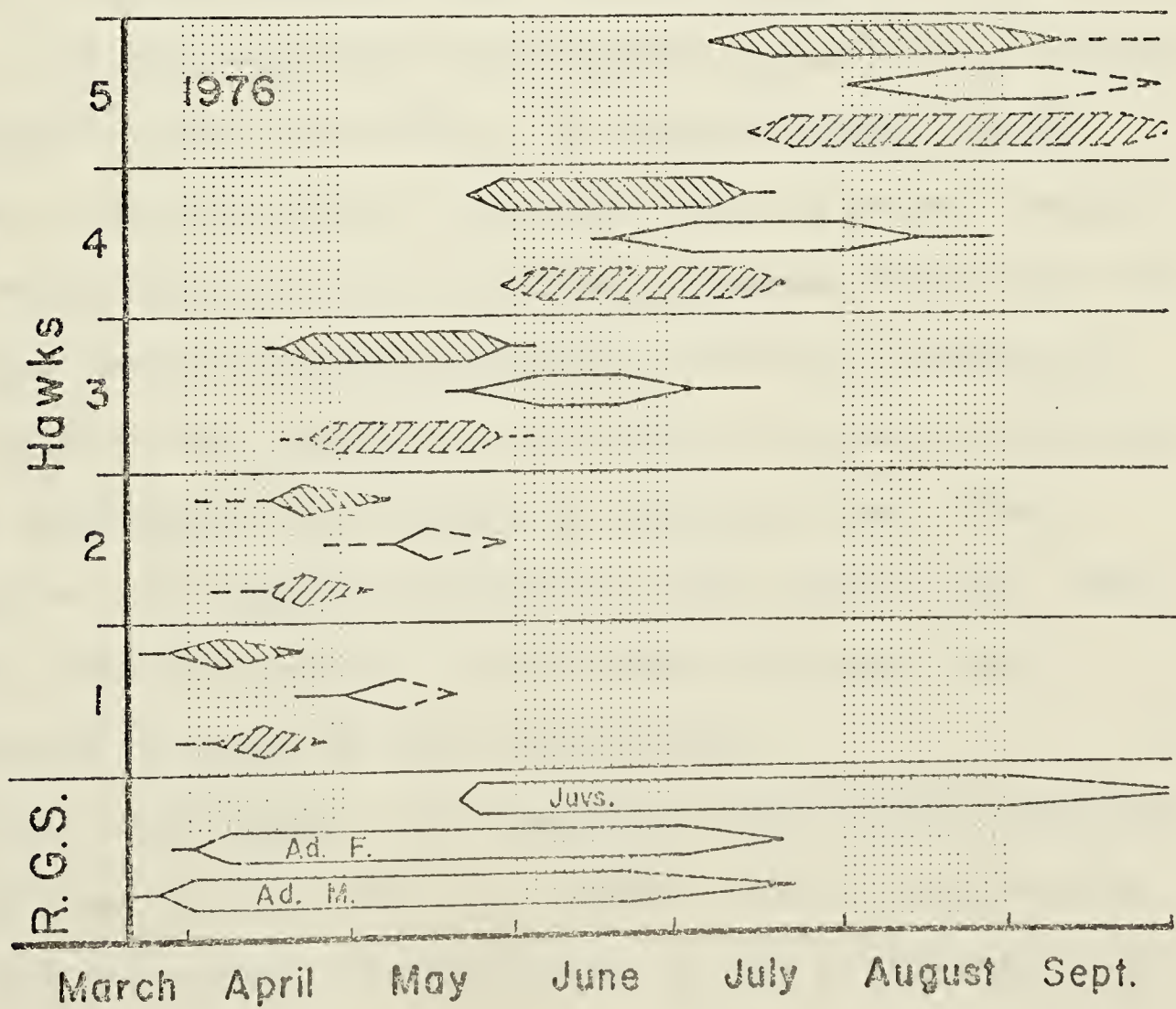
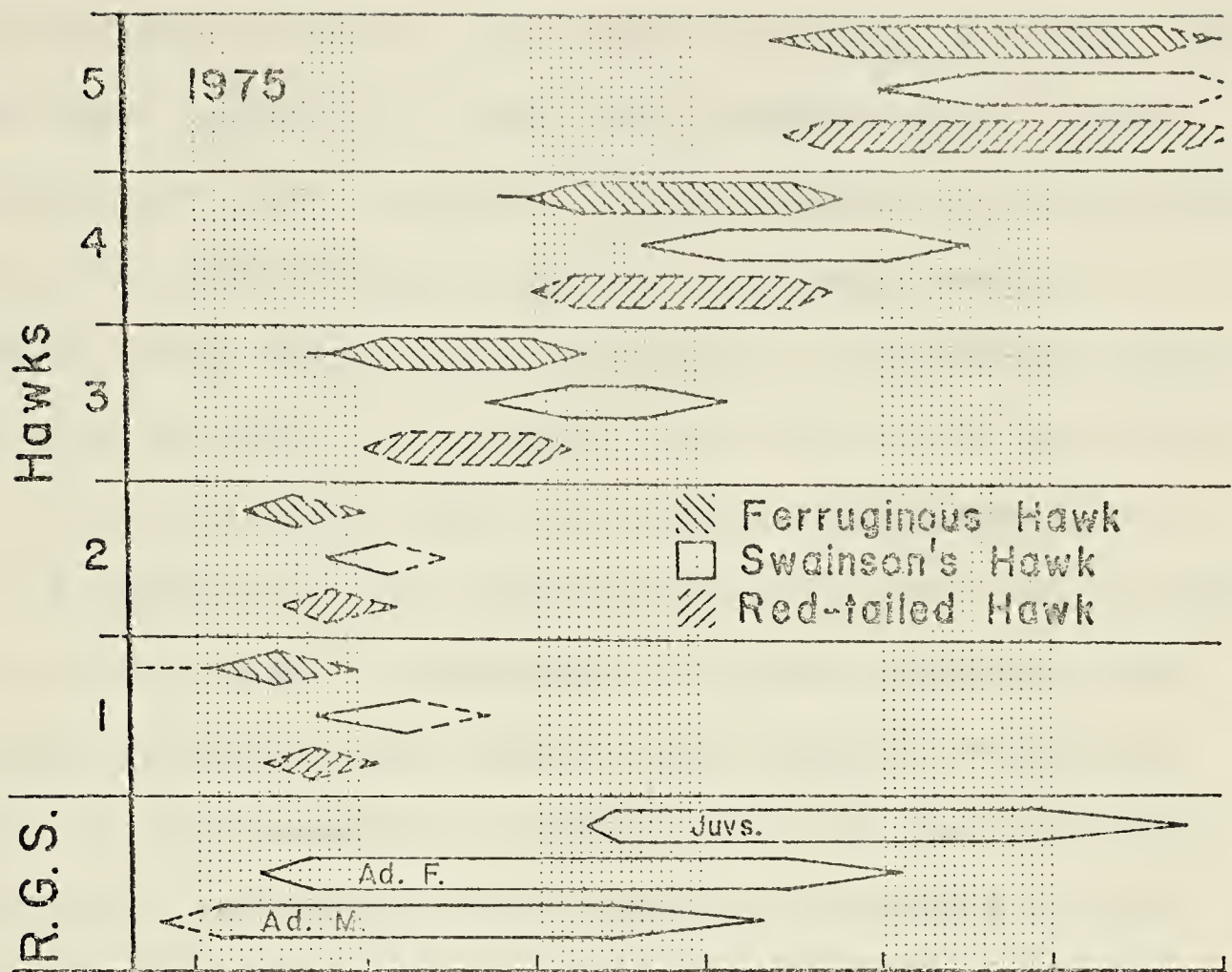
Seasonal Overlap

There are three factors which may be important in determining the timing of breeding. Firstly, breeding periods are limited to the summer months in those areas where summers are short (Raymont 1963, Bédard 1969). Secondly, abundance of food may influence breeding times. Lack (1966) has suggested that young hatch when food is most abundant. Thirdly, if two or more species use the same resource, breeding times may be staggered to allow each species exclusive use of the food resource at a particular time (MacArthur 1958, Cody 1974, Clark and Ward 1974).

All three species of hawks considered in this study migrate into temperate regions to breed and therefore must do so during the summer months. Further, they all prey heavily on Richardson's ground squirrels which are available only during the nonhibernating period which extended on the study area from late March to early October (S. Schmutz 1977). Therefore these species are constrained by both migration and food availability to breed during the summer months. Within these constraints breeding periods cannot be greatly staggered.

Fig. 6 illustrates the major events in the breeding cycle of ferruginous, Swainson's and red-tailed hawks on the study area. The date of first arrival of ferruginous hawks was not known in 1975 because they were already present on the study area when I arrived on April 11. The dates of

Figure 6. Chronology of breeding events of the three species of hawks in 1975 and 1976; arrival on the study area (1), courtship and nestbuilding (2), incubation (3), nestling period (4), postfledging period (5). The above-ground period of Richardson's ground squirrels (R.G.S.) is portrayed separately for adult males (Ad. M.), adult females (Ad. F.) and juvenile males and females (Juvs.). Broken lines are used when no data are available but the particular phenomenon is presumed to occur or when the sample size is low, as in the case of red-tailed hawks. Solid lines before and after a bar represent one observation per day at the onset and termination of a breeding event.



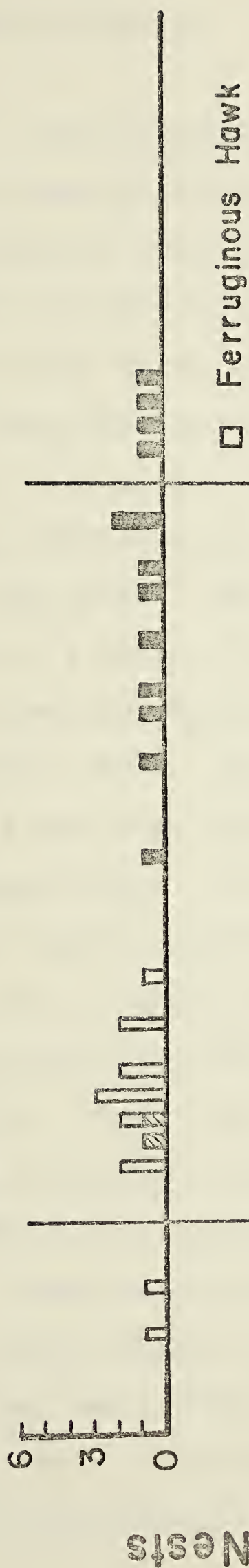
departure from the study area were not known in either year because some individuals were still present when I left. Competition for food probably is most likely to occur during nestling and postfledging periods. Although young Swainson's hawks hatch later than young ferruginous hawks, the overlap of these two periods was 82% in 1975 and 73% in 1976. It was unlikely that this small displacement is a result of competition for food because food was not in short supply at that time. Richardson's ground squirrels, the main prey, reproduce only once a year (Howell 1938) and therefore a postponement of breeding by one species means that the prey population will already be reduced by the other species (Lack 1971). Ricklefs (1966) found that breeding periods among closely related sympatric species of birds, in both temperate and tropical regions consistently overlapped by more than 90%. In eastern Africa, four species of eagles did not displace their breeding periods even though they were not migratory (Smeenk 1974) but bred at a time when the prey population was also reproducing. This suggests that abundance of food is the most important factor determining the timing of breeding (Lack 1966). During the reproductive periods of prey populations, food for the hawks is probably sufficiently abundant that competition is only of minor importance.

Young ferruginous hawks hatched significantly earlier in 1976 than in 1975 ($F=5.65$, $P<0.01$) whereas Swainson's hawks did not differ significantly in the distribution of

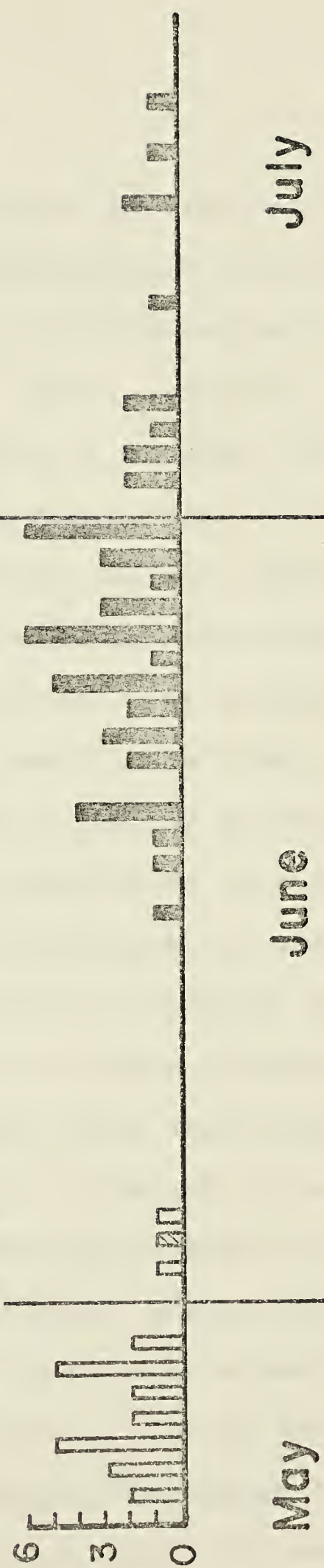
hatching dates between years ($F=0.21$) (Fig. 7). Young Richardson's ground squirrels emerged earlier in 1976 which suggests that a common environmental stimulus synchronizes the timing of breeding of one of the predators (ferruginous hawks) and its main prey.

Figure 7. Distribution of hatching dates of the three species of hawks in 1975 and 1976. Dates represent the day on which the first nestling hatched (backdated using the length of primary remex number four-Appendix 2) for ferruginous and Swainson's hawks. Hatching dates of nestling red-tailed hawks were estimated on the basis of nestling size when less than 2 weeks of age.

1975



1976



July

June

May

Spatial Overlap

Territoriality

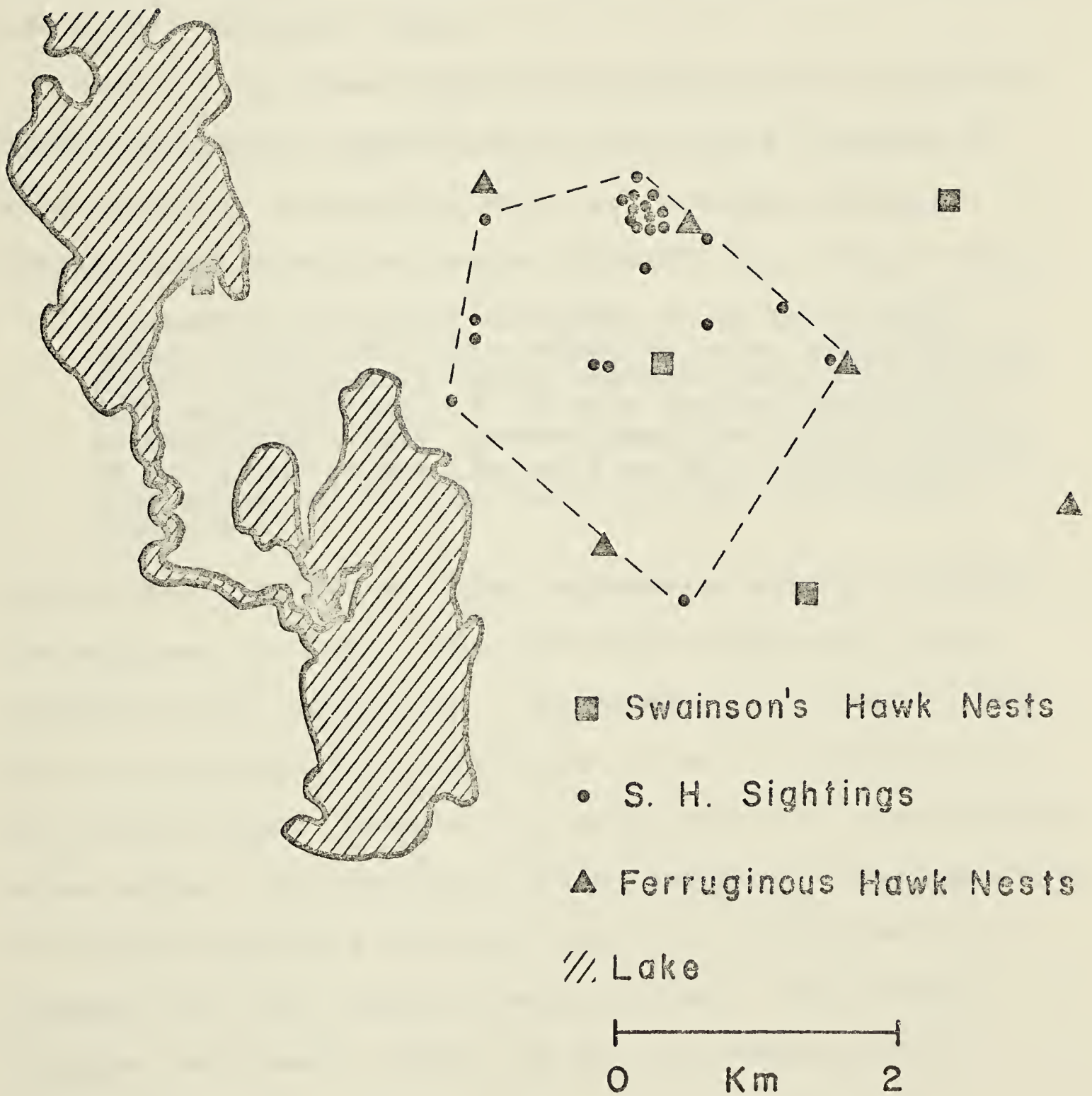
In communities where food resources of birds are distributed in three dimensions, interspecific competition for food is reduced through vertical stratification of feeding zones (Gibb 1954, MacArthur 1958). However, when two or more species are forced to feed on a common food resource that is located in only two dimensions, such vertical stratification is not possible (Orians and Wilson 1964, Cody 1974). This latter situation applies to many species of raptors, buteos in particular, that feed on ground-dwelling vertebrates (Orians and Wilson 1964, Brown and Amadon 1968). Coexistence of such species may be possible when they maintain mutually exclusive territories (Hutchinson 1958). Interspecific territoriality would be expected between species that are unable to achieve enough separation in feeding zones or food to permit coexistence (Orians and Wilson 1964, Ashmole 1968, Cody 1969, Emlen et al. 1975). Under such circumstances, it should not matter to a pair holding a territory whether the adjacent territory is occupied by the same or another species (Hutchinson 1958). Hawks usually defend only a small area around their nests, their nesting territory, located inside an area over which they hunt, their home range (Brown and Amadon 1968, Newton 1976). To calculate the average amount of space available per pair, I divided the size of the study area by

the total number of nesting pairs. This resulted in 4.4 km² available per pair in 1975 and 3.7 km² in 1976.

Observations of hawks on the study area suggested that their home ranges overlapped considerably, at least interspecifically. In order to estimate the degree of overlap of home ranges, four adult ferruginous and eight adult Swainson's hawks were color-marked. Only one pair of Swainson's hawks was observed sufficiently often to permit a reasonable estimate of the size of their home range. This was calculated by plotting the locations of 25 sightings on a map and connecting the outermost points (Newton 1976) to give a home range of 6.2 km² (Fig. 8). That portion of the study area which one pair of buteos could potentially use exclusively was 4.4 km² in 1975 and 3.7 km² in 1976. Since areas available per pair in both years were much smaller than the 6.2 km² used by one color-marked pair of Swainson's hawks, home ranges probably overlapped extensively. Furthermore, individuals of each species were observed in the same area at different times indicating spatial, if not temporal, overlap.

Overlap of home ranges is generally the case among hawks (Brown and Amadon 1968, Newton 1976). Smith and Murphy (1973) mapped home ranges of 25 pairs of ferruginous hawks and of five pairs of Swainson's hawks. Based on an examination of their maps, each home range of a pair of Swainson's hawks overlapped that of a pair of ferruginous hawks in central Utah, in one instance the overlap appeared

Figure 8. Locations of observations made in 1975 of a nesting pair of Swainson's hawks that was color-marked. The locations of nearby pairs of ferruginous and Swainson's hawks are included and the lakes, for orientation (Fig.1).



almost complete. The home ranges of ferruginous hawks averaged 5.2 km² (n=9) and 6.5 km² (n=5) and those of Swainson's hawks, 4.7 km² (n=2) and 3.0 km² (n=1), in 2 years of their study (Smith and Murphy 1973). Defense of such large areas is not feasible from the standpoint of time and energy (Schoener 1968).

Even if the home ranges of ferruginous and Swainson's hawks overlapped, competition for food may be reduced to some degree by maintaining mutually exclusive nesting territories. Brown and Amadon (1968:85) have stated that:

"...nesting territory in hawks, as in other birds, seems to have its basis primarily as an adaptation to reduce or eliminate sexual disturbance or competition from unpaired birds of the same species during the reproductive cycle. Nevertheless the classic concept of territory as ensuring an area containing adequate food resources for the brood of young may also be involved."

Territorial disputes or actual aggressive behavior between ferruginous, Swainson's and red-tailed hawks were rarely observed on the study area. Occasionally Swainson's hawks were seen stooping at individuals of both ferruginous and red-tailed hawks. However this aggression was observed most often while I was analyzing prey at nests of ferruginous and red-tailed hawks and hence may have been influenced by my presence (R. Fyfe personal communication). Territorial behavior is probably subtle and may be communicated by postures (Weir and Picozzi 1975) not easily observed. Therefore, nesting territories may be defended with little observable overt aggression.

The existence of nesting territories may be deduced from the dispersion of nesting pairs (Fig. 9). Since only two pairs of ferruginous hawks and one pair of Swainson's hawks nested on the ground in both years and trees were sparse, the dispersion of nesting pairs was highly correlated with the availability of trees. Intraspecific dispersion of nesting pairs was therefore dependent on 1) the availability of trees and 2) social interaction. Fig. 10 shows that ferruginous and Swainson's hawks nested no closer than 0.8 km and 0.7 km respectively from neighbors of the same species. This was not merely a reflection of the availability of nest sites because, interspecifically, they nested closer together. Two pairs of red-tailed hawks nested 0.5 km from each other (Fig. 10). This may have been a polygamous situation since on the first visit to these nests, a total of only three red-tailed hawks were associated with both nest sites. On the second visit only one nest was occupied and the nestlings from the other nest had disappeared. Red-tailed hawks also appeared to nest closer to pairs of other species than pairs of their own although the sample size was too small to confirm this.

It is possible to estimate the minimum size of the nesting territories of ferruginous and Swainson's hawks. Since ferruginous hawks nested no closer than 0.8 km and Swainson's hawks no closer than 0.7 km from each other, the minimum radii of their nesting territories were 0.4 km and 0.35 km respectively. This assumes that the nesting

Figure 9. Locations of nests of ferruginous, Swainson's and red-tailed hawks on the study area (Fig.1). One symbol inside another indicates that the same nest was used by the same or another pair of the same or another species in the second year.

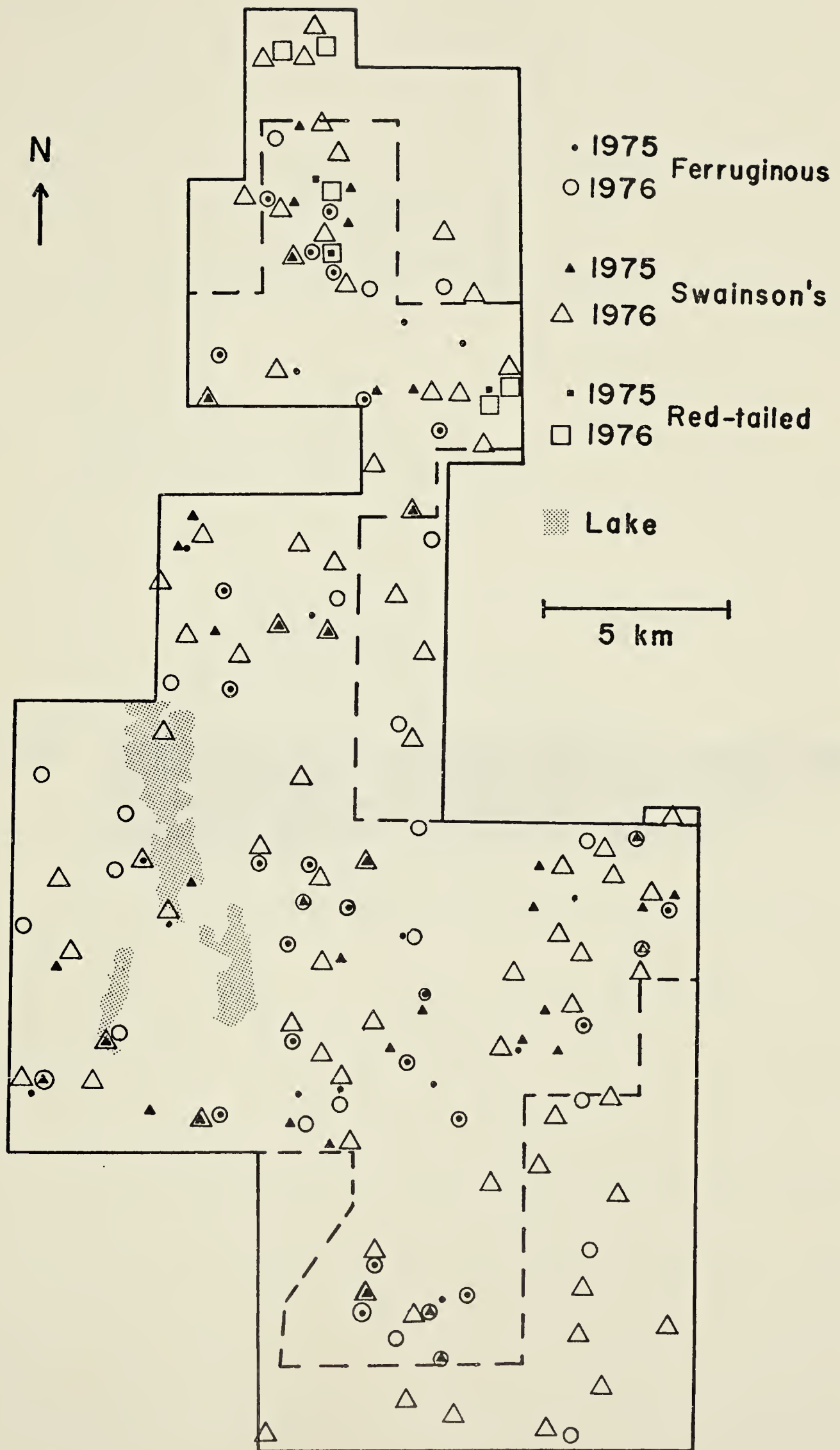
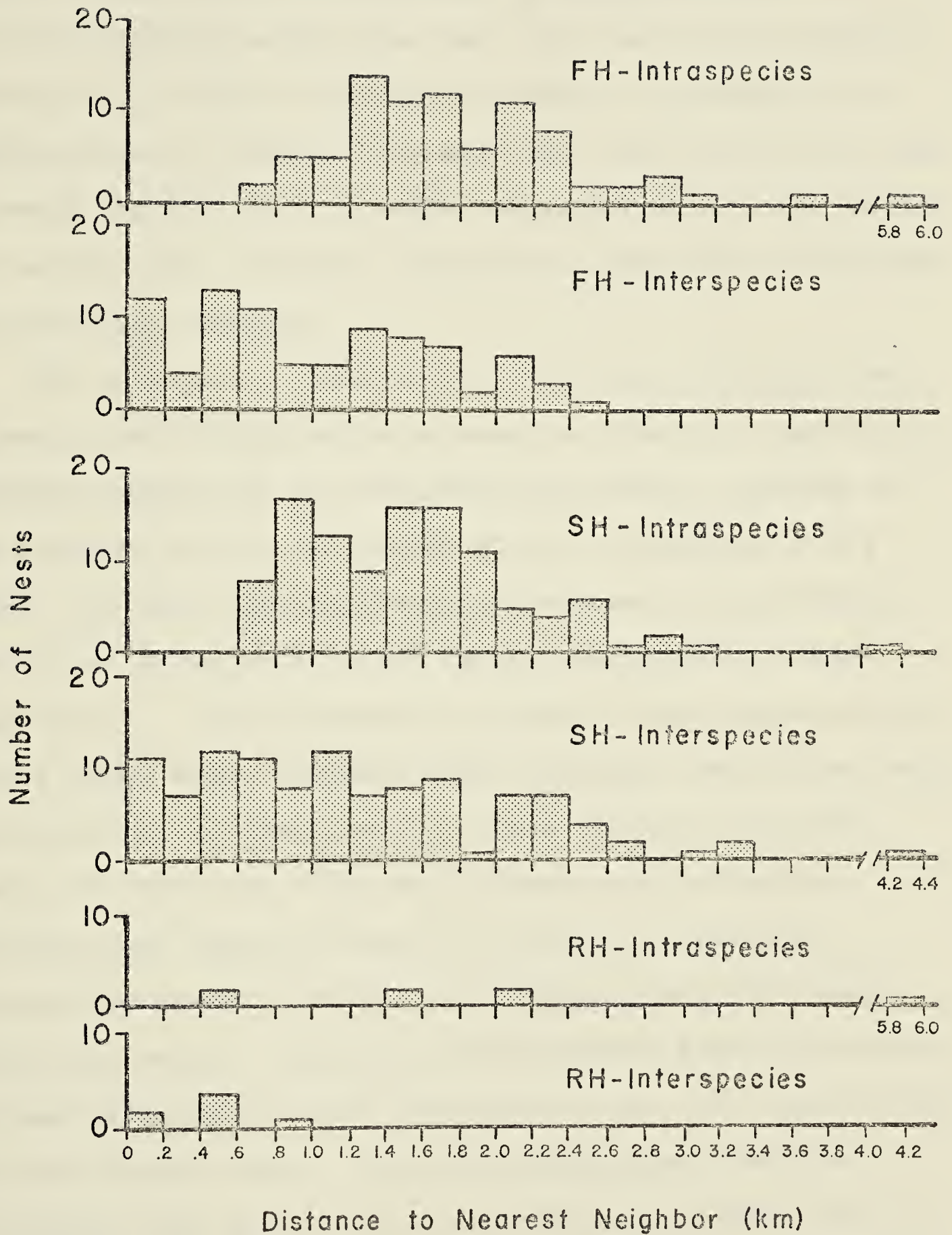


Figure 10. Distances between occupied nests of ferruginous (FH), Swainson's (SH) and red-tailed hawks (RH) and their nearest neighbors of the same and different species, both years combined.



territories were circular and that the nest site was in its center. Under these assumptions the minimum size of a nesting territory would have been 0.5 km² for ferruginous hawks and 0.4 km² for Swainson's hawks. The density of nesting buteos, however, was much less than would have been expected had the nesting pairs defended only an area of 0.5 km² and 0.4 km². Why was the nesting population maintained at this lower density?

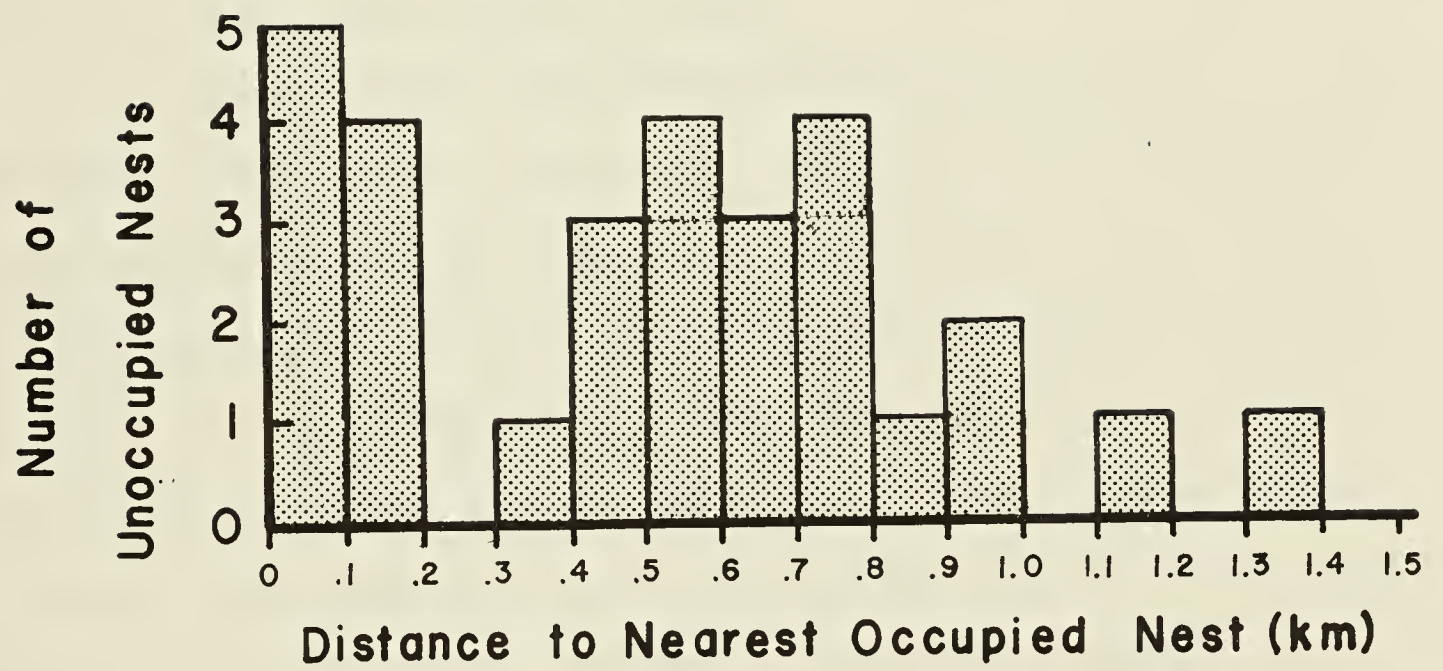
The paucity of trees on the study area suggests that potential nest sites may have been the resource limiting the breeding density of at least the tree nesting species, as was presumed on the shortgrass plains of Colorado (Cody 1974). To test this hypothesis, I erected 93 artificial nest sites on an area of 100 km² in the autumn of 1975 (Appendix 4). This created an excess of nest sites on part of the study area, assuming such artificial nest sites would be acceptable to these hawks. Parts of this area were devoid of trees and other parts contained previously occupied nest sites in trees. In 1976, two pairs of ferruginous hawks nested on and fledged young from these artificial nests. Two pairs of Swainson's hawks also nested on these artificial sites but only one pair was known to lay eggs and fledge young. Thus, the assumption that the artificial nest sites would be sufficiently attractive to induce at least some pairs of both ferruginous and Swainson's hawks to nest on them was validated. However, this in itself is insufficient evidence to suggest that the

breeding population was increased significantly by erection of artificial nest sites unless it could be shown that the number of breeding pairs was increased in the area where nest sites were erected, over the number breeding outside this area.

In that part of the study area where artificial nest sites were erected, seven pairs of ferruginous hawks and five pairs of Swainsons hawks were found nesting in 1975. In 1976, nine pairs of ferruginous hawks and eight pairs of Swainson's hawks were found nesting in the same area. This represents an increase of 42% (12 in 1975 to 17 pairs in 1976). On the part of the study area where no artificial nest sites were erected, the number of breeding ferruginous hawks also increased from 31 to 33 pairs and Swainson's hawks, from 31 to 45 pairs, a total increase of 26%. The increases on these two parts of the study area were not significantly different ($G=0.007$). Of 93 artificial nest sites, 87 were not occupied by any species of bird (two were occupied by crows (Corvus brachyrhynchos), four by hawks). Thus, it is unlikely that the breeding population was limited by the availability of nest sites, except perhaps very locally.

In addition to 87 artificial nest sites, 28 natural nest sites occupied by either ferruginous, Swainson's or red-tailed hawks in 1975, were not occupied in 1976. Of these 28 sites, 23 were located less than 0.8 km from other occupied sites (Fig. 11), the distance below which pairs of

Figure 11. Distances of nests, occupied in 1975 but unoccupied in 1976, from the nearest nest occupied by any pair of the three species.



the same species were not observed to nest (Fig. 10). This suggests that considerable space around the nest site was defended by each resident pair and that most unoccupied sites were within this space.

These observations suggest that the breeding populations of ferruginous and Swainson's hawks may have been limited by territorial behavior. Three conditions must be met before it can be concluded that territorial behavior limits the numbers of a breeding population in any one year (Watson and Moss 1970, Klomp 1972).

The first of these conditions states that "[a] substantial part of the population does not breed, either because animals die; or because they attempt to breed but they, and/or their young all die; or because they are inhibited from breeding even though they survive, and may breed in later years" (Klomp 1972:460). Ferruginous hawks that might have been part of a non-breeding cohort were not observed in either year. However, Swainson's hawks, presumed to be subadults because they were not in the typical adult plumage (Brown and Amadon 1968), were observed on the study area in both years. These seemingly were not associated with any particular part of the study area and did not appear to be breeding. On one occasion 13 were seen in one field. One pair of Swainson's hawks, in subadult plumage, was trapped using prey as a lure (Berger and Mueller 1959). This pair, although repeatedly seen in the same locality, did not appear to be nesting. These

observations suggest that subadult Swainson's hawks, which did not breed, were nevertheless present on the study area.

The second condition states that "[s]uch non-breeders are physiologically capable of breeding if the more dominant or territorial (i.e., breeding) animals are removed" (Klomp 1972:460). I caught and removed two paired male ferruginous and three male Swainson's hawks from their respective territories at the time of laying to determine if surplus individuals were present to replace them. One female ferruginous hawk deserted the nest site after the male and four eggs were removed. The other female remained after the male and one egg were removed and laid a second egg which was incubated until it hatched. One of the males that had been color-marked and released about 90 km away, returned within 11 days, prior to which no replacement was noted. This supports the previous contention that surplus ferruginous hawks were not present on the study area but the data are inconclusive. The three Swainson's hawks trapped were kept in captivity to avoid the possibility of their returning to the study area after release. After the removal, extensive courtship was observed in the vicinity of their previous nest sites. Two Swainson's hawks were seen again at these three nest sites between 1 and 4 days after removal of the three males. One individual at one of these sites was seen sitting low in the nest, as though incubating, 20 days after the removal. At this site, two Swainson's Hawks responded vigorously to a tethered intruder

33 days after removal. At the time when hatching should have occurred this pair was no longer present. Disturbance by the landowner, who was shooting nesting corvids in this area, may have caused the hawks to desert. The other two nests, where males were removed, were apparently deserted as there was no evidence of eggs, young or adult hawks at the time when eggs should have hatched. However, young fledged from a nest 0.5 km from one of these latter nests. This pair may have moved from the nest where the first male was removed to a nearby unoccupied nest. These observations strongly suggest that all three Swainson's hawks were replaced. One male that moved in after the removals was in adult plumage and the other two were never seen close enough to determine the pattern of their plumage. Swainson's hawks in subadult plumage are physiologically able to breed because two males, trapped at nest sites containing young, exhibited subadult plumage.

The third condition states that "[t]he breeding animals are not completely using up some resource, such as food, space, or nest sites. If they are the resource itself is limiting" (Klomp 1972:460). Evidence cited previously suggested that food and nest sites were not in short supply.

Although there is no evidence to suggest the presence of nonbreeding ferruginous hawks, breeding pairs of this species spaced themselves uniformly (Fig. 10). Such a spatial distribution suggests that the breeding population was dispersed by territorial behavior. For Swainson's hawks

all three conditions were met and therefore the density of breeding pairs each year appears to be limited by intraspecific territorial behavior.

According to Hinde (1956) territoriality serves to provide a nest site with space to perform reproductive activities, food for the pair and their young, familiar cover to avoid predation and it serves to limit densities and thus avoid overpopulation. The use of cover to avoid predation is probably unimportant for hawks. The limitation of numbers by territorial behavior, to prevent overpopulation, is only a secondary consequence of other advantages accruing to individuals as the result of spacing behavior (Brown 1969). If the limitation of density is a by-product of territoriality and concealment from predators is unimportant to hawks then territoriality must have evolved through increasing the fitness of individuals that possessed a territory that provided them with space and nest sites for successful reproduction. The density of breeding buteos recorded was much lower than theoretically could have been supported by food alone since less than 15% of the total population of Richardson's ground squirrels was taken by nesting buteos. This suggests that the size of territories was not determined by available food supply (Murray 1971, Welsh 1975) but by a minimum requirement for space.

Territories are maintained intraspecifically by each species but not interspecifically (Fig. 10). Interspecific

territoriality is not expected between two species "if the species are so different that the effort required for this mutual exclusion is not compensated for by increased access to resources..." (Orians and Wilson 1964:737). Ferruginous and Swainson's hawks use the same food resource and therefore it is surprising that they do not maintain interspecific territories more effectively. Despite ineffective interspecific territoriality, the numbers of breeding butoes was still below the level at which competition for food was affecting their reproductive performance. However, it is possible that pairs of different species, when nesting in close proximity, interfere with each other in their reproductive activities and in the care of their young to the extent that their reproductive performances are reduced.

Interspecific Interactions

In previous studies of interspecific competition, decreased reproductive efficiency and growth rate have been attributed to competition (Connell 1970, Ameyaw-Akumfi 1975, Bach et al. 1976). I investigated the effect of one species on the other's nesting success, reproductive performance and growth rate of nestlings by comparing these parameters for each species nesting at high and low densities.

Nesting Success

Not all nesting attempts on the study area were successful. Of 38 nesting attempts by ferruginous hawks in 1975, 26 (68%) fledged young. In 1976, of 50 attempts, 23 (46%) fledged young. This difference between years approached significance ($G=3.58$, $p<0.1$). Of 35 nesting attempts by Swainson's hawks in 1975 where the reproductive success was known, 27 (77%) were successful in fledging young and of 77 attempts in 1976, 56 (73%) fledged young. The difference in fledging success between years among ferruginous hawks, but not Swainson's hawks, probably reflects the fact that early nests of the former species that failed were not recorded in 1975. Field work began earlier and greater familiarity with available nest sites facilitated finding early nesting attempts, both successful and unsuccessful, in 1976.

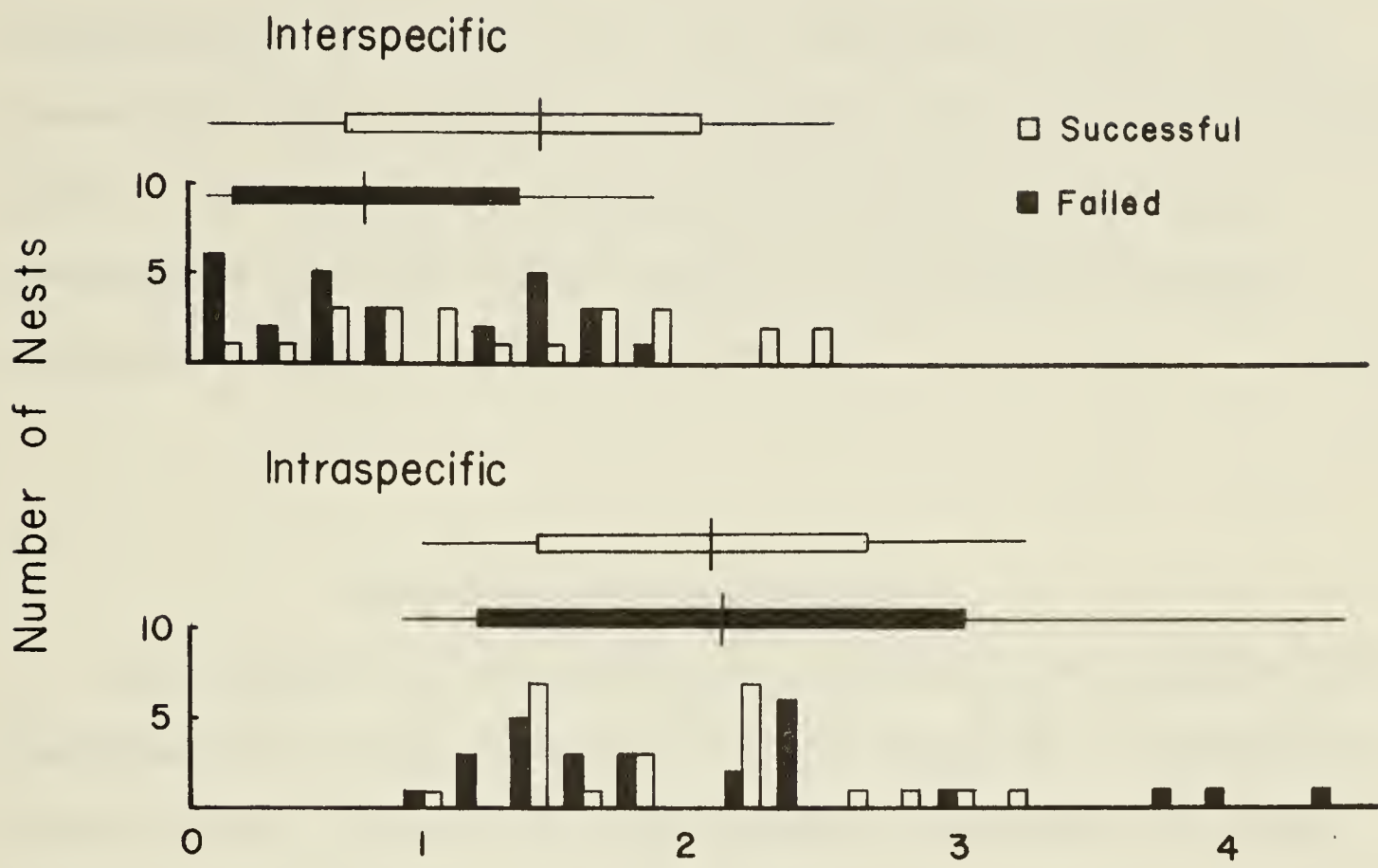
Of a total of 68 nesting failures of both ferruginous and Swainson's hawks during both years, three clearly resulted from removing the male hawks, one probably from disturbance by the landowner and one from the use of time-lapse cameras. Although nine of the remaining 63 nesting failures could be attributed to disturbance resulting from visits to nests and nine to nests falling from trees during storms, 45 nests were unsuccessful in fledging young for no apparent reason. Since both ferruginous and Swainson's hawks nested closer to the other species than to their own species it is possible that interspecific aggression caused

some nesting failures. I plotted the distances to nearest neighbor and compared the distribution of successful versus unsuccessful nests (Fig. 12). Only nests occupied in 1976 were used because I was confident that all nesting attempts were recorded during that year. Distances to nearest neighbor of the other species were significantly greater for successful than for unsuccessful nests (ferruginous hawk, $F=6.63$, Swainson's hawk, $F=4.16$, $p<0.05$). On the other hand distances to the nearest neighbor of the same species were not significantly different for successful than for unsuccessful nests (ferruginous hawk, $F=0.26$; Swainson's hawk, $F=0.77$, $p>0.05$). This suggests that the nesting success of both species is lowered when they nested closer to each other than each species nested intraspecifically.

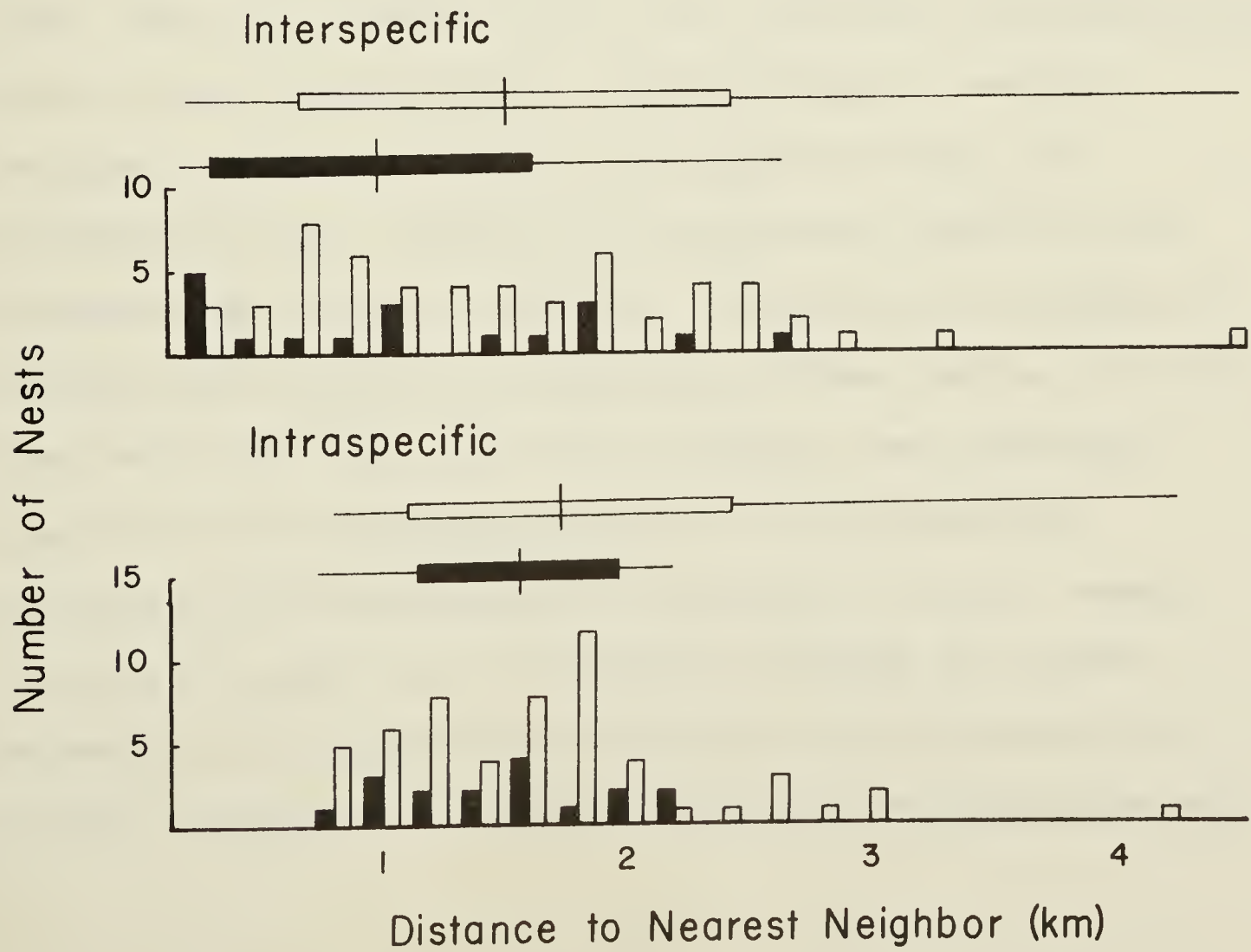
Interactions between the two species appeared to be exhibited in aggressive interference, particularly during the early part of the nesting cycle. This was probably because each species constantly trespassed into the nesting territory of the other which elicited aggressive encounters and, in some cases, eventually desertion of nests. A pair of Swainson's hawks built a nest in a row of planted trees approximately 5 meters from a nest occupied by a pair of ferruginous hawks. Aggressive interactions were observed in the vicinity of these nests. Shortly before the time the ferruginous hawks should have hatched they deserted their nest. Another nest of ferruginous hawks also found deserted at the time of hatching, was 0.6 km from a nest of

Figure 12. Number of successful and unsuccessful nests in relation to their nearest neighbor of the same and different species. Horizontal bars show the mean plus and minus one standard deviation and the range of the distributions.

Ferruginous Hawk 1976



Swainson's Hawk 1976



Swainson's hawks. Hawks were also seen interacting aggressively in flight near both these nest sites. The combatants met in midair and tumbled down holding on to each other. Interspecific aggression between ferruginous, Swainson's and red-tailed hawks has also been observed elsewhere (Angell 1969, Platt 1971).

Reproductive Performance

The effect of interspecific proximity on reproductive performance of each species was investigated by comparing clutch size, percent of eggs hatched and number of young fledged with distance to nearest neighbor and with density of nesting hawks. Measurements of distances between nests included all but two nests known to have been occupied in 1976. The two excluded nests were apparently abandoned very early in the nesting cycle. The distance to nearest neighbor takes into account the impact of only one neighboring pair. However the cumulative impact of all neighbors may be more important. Therefore the number of nesting pairs within an arbitrarily chosen radius of 1.6 km from each nest site was used to measure the cumulative impact of all neighboring pairs on the reproductive performance of ferruginous and Swainson's hawks. Among ferruginous hawks the relationships between the three parameters of reproductive performance and distances to nearest neighbors, as well as density of nesting pairs were

not significant (Table 8 and 9). Among Swainson's hawks the relationships between two parameters of reproductive performance (clutch size and the number of young fledged) and distances to nearest neighbors, as well as density of nesting pairs were not significant (Tables 8 and 9). However, the relationships between percent of eggs hatched and the distance to nearest neighbor, as well as density of nesting pairs, were significant (Tables 8 and 9). This suggests that where Swainson's hawks nested in close proximity to the same or other species, their hatching success was lower.

Growth Rates of Nestling Hawks

Since interspecific aggression influences the nesting success of the hawks it also may reduce the amount of time pairs spend caring for their young. Reduced hunting time, because of intraspecific and interspecific encounters, could influence the growth rate of young. To investigate this possibility, body weight of nestlings was plotted against distances to nearest neighbor and against nest densities. Nestling body weight per se could not be used because of the inherent difference in body weight between males and females, thus necessitating the use of a correction factor (Appendix 4). The relationship between weight of nestling ferruginous hawks and the distance to nearest neighbor (both of the same and other species) was significant (Table 10).

Table 8. The relationship between reproductive performance of ferruginous and Swainson's hawks and distance to nearest neighbor in 1976. Clutch size was recorded from successful and unsuccessful nests in which eggs or young less than 1 week old were found. Percent hatched was calculated from nests in which the clutch size and the number hatched was known. The number of young fledged was weighted to include those nestlings which died before fledging because a pair, raising a chick to near fledging age, was presumably more successful than one raising a chick only 0.3 of the nestling period. For those nests, in which the number hatched was not known, only the number present at the time of fledging was used.

	Correlation Coefficient	
	Distance Between Same Species	Distance Between Other Species
Ferruginous Hawk		
Clutch Size (n=27)	0.109	0.258
Percent Hatched (n=26)	0.191	0.131
Number fledged (n=28)	-0.049	0.298
Swainson's Hawk		
Clutch Size (n=31)	0.038	0.218
Percent Hatched (n=31)	0.305*	0.436**
Number Fledged (n=52)	0.039	0.225

*= $p < 0.05$, **= $p < 0.01$

Table 9. The relationship between reproductive performance of ferruginous and Swainson's hawks and density of nesting pairs in 1976. See Table 8 for details on reproductive parameters.

	Correlation Coefficient	
	Density of Same Species	Density of Other Species
Ferruginous Hawk		
Clutch Size (n=27)	-0.232	-0.095
Percent Hatched (n=26)	-0.288	0.076
Number Fledged (n=28)	0.160	-0.067
Swainson's Hawks		
Clutch Size (n=31)	0.119	0.079
Percent Fledged (n=31)	-0.339*	-0.325*
Number Fledged (n=52)	-0.021	-0.128

*= $p < 0.05$

Table 10. The relationship between body weight of nestling ferruginous (n=49) and Swainson's hawks (n=82) and distance to nearest neighbor and density of nesting pairs in 1976.

Nestling	Correlation Coefficients	
	Distance Between Same Species	Distance Between Other Species
Ferruginous Hawks	0.288*	0.342**
Swainson's Hawks	0.088	0.171
Nestling	Density of	
	Same Species	Other Species
Ferruginous Hawks	-0.176	-0.415**
Swainson's Hawks	-0.247*	-0.269**

*= $p < 0.05$, **= $p < 0.01$

Among Swainson's hawks this relationship showed no significant correlation. When weights of the nestlings of these two species were plotted against density of nesting hawks, both showed significant inverse relationships (Table 10). Although the correlation coefficients were low, this suggests that the proximity of nesting pairs was not only related to the success or failure of nests but also to the hatching success of Swainson's hawks and to the weights of nestlings of both species.

Interspecific Territoriality

These results suggest some form of behavioral conflict which probably would be minimized or abolished entirely if these species were to maintain mutually exclusive interspecific territories. The question arises; why are interspecific territories not established and maintained? It is possible that Swainson's hawks can establish nesting territories nearer to ferruginous than to other Swainson's hawks because the level of territorial aggression in ferruginous hawks, which nest earlier, may have waned (Catchpole 1973) by the time Swainson's hawks arrive and establish territories. To determine whether levels of aggression wane after laying, captive hawks were tethered near occupied nest sites of ferruginous and Swainson's hawks in 1976 and the responses of the resident pairs recorded. It was not possible to test the aggressive responses of

ferruginous hawks at two different times, for instance, 1 week before and 2 weeks after laying, because captive hawks and the necessary permits were not obtained in time to do this. Thus ferruginous hawks were tested only after laying. However, it was possible to test the aggressiveness of Swainson's hawks both before and after laying (Fig. 13) because they nested later. The responses of Swainson's hawks did not change significantly between the two periods (Kolmogorov-Smirnov Two Sample Test, $p > 0.05$). I believe it is unlikely that the levels of aggressiveness shown by ferruginous hawks would have changed either. Furthermore, ferruginous and red-tailed hawks arrive at about the same time on the study area and also nest in close proximity to one another; an explanation for this proximity based on a waning of aggression seems unlikely. Therefore, I believe that a waning of aggression in ferruginous hawks is not a valid hypothesis to explain the close proximity of nests between ferruginous and Swainson's hawks.

Swainson's hawks were significantly more aggressive intraspecifically (Kolmogorov-Smirnov Two Sample test, $p < 0.05$) than ferruginous hawks (Fig. 13). Only four trials were run, to test the responses of Swainson's hawks to a tethered ferruginous hawk before the former's incubation period was over. The results showed that Swainson's hawks were significantly more aggressive ($p < 0.05$) toward ferruginous hawks than the latter were toward either Swainson's or red-tailed hawks. Therefore Swainson's hawks

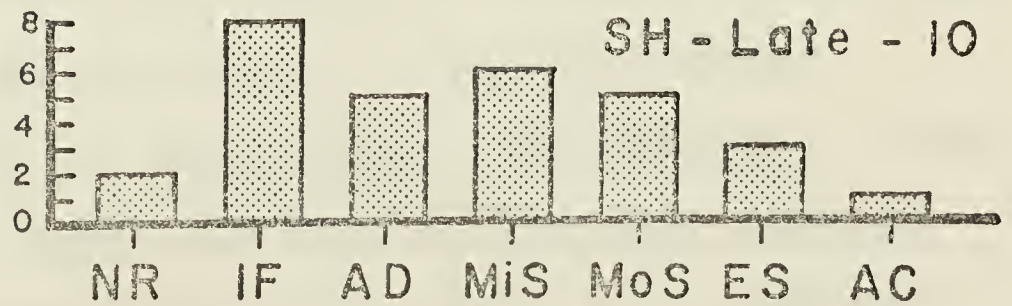
Figure 13. Responses of nesting pairs of ferruginous and Swainson's hawks to a tethered ferruginous (FH), Swainson's (SH) and red-tailed hawk (RH). The responses recorded were; no response (NR), investigative flight (IF), aggressive display (AD), mild stoop (MiS), moderate stoop (MoS), extreme stoop (ES) and aggressive contact (AC). Although pairs may have exhibited a response several times, only one response within each category is portrayed. At nests of ferruginous hawks, a ferruginous hawk (FH) was tethered between 5 and 19 days (mean=14) after laying, a Swainson's hawk (SH) between 20-30 days (mean=26) and a red-tailed hawk (RH) between 8-20 days (mean=15) after laying. At nests of Swainson's hawks, a ferruginous hawk was tethered between 18-7 days (mean=12) before laying, a Swainson's hawk for the first time (Early) between 17 before and 5 days after (mean=10 before) laying and a Swainson's hawk the second time (Late) between 12-30 days (mean=21) after laying.

Number of Responses by Pairs of

Ferruginous Hawks



Swainson's Hawks



Responses

appeared to be more aggressive both interspecifically and intraspecifically than ferruginous hawks. Swainson's hawks exhibited many extreme stoops and even actual aggressive contacts against the staked intruder, responses that were never exhibited by ferruginous hawks. One observation period had to be prematurely terminated because I feared that a resident pair would injure the tethered Swainson's hawk during aggressive contacts. This greater aggressiveness of Swainson's hawks was sufficient to explain the difference in the distances recorded to nearest nests of the same versus the other species (Fig. 10). This greater aggressiveness may have contributed to reduced hatching success. The close proximity of other pairs may have elicited frequent aggressive responses and thereby reduced the time spent incubating.

If decreased reproductive success among pairs of ferruginous and Swainson's hawks had resulted whenever they nested in close proximity, I would expect that a strong selective advantage would have accrued to those pairs that nested outside the nesting territory of other pairs. Those pairs of ferruginous hawks that were able to exclude Swainson's hawks from their nesting territories would have been more successful reproductively and this should ultimately have led to interspecific territoriality. There are at least two reasons why this may not have occurred. Since ferruginous and Swainson's hawks are not sympatric over their entire breeding range, gene flow between areas of

sympatry and allopatry may prevent effective evolution of interspecific territoriality (Stebbins 1971). The other possibility is that ferruginous and Swainson's hawks may have only relatively recently become as widely sympatric as they are now, through the alteration of the prairie habitat by man. Hence, insufficient time has elapsed for selection to have resulted in the degree of interspecific territoriality necessary to exclude Swainson's hawks from the nesting territories of ferruginous hawks.

Habitat

Birds are ecologically segregated most commonly by occupying different habitats (Lack 1971). Differences in habitat selection observed today presumably have resulted either from competition in the past (Lack 1971) or through geographical isolation (Stebbins 1971). These ultimate factors gave rise to the differences in habitat selection exhibited by extant species. This selection of appropriate habitat is proximally determined by physiological or psychological preferences (Lack 1971).

Although ferruginous, Swainson's, and red-tailed hawks overlap broadly in their breeding range it is possible that each species has a different optimal nesting habitat within this broad breeding range. This possibility suggested itself initially during this study in two ways. Firstly, red-tailed hawks were found nesting only in the northern part of the study area where aspen trees, growing around permanent and semipermanent ponds, were much more numerous. On the study area, red-tailed hawks constituted 5% (6 of 133) and ferruginous hawks 38% (50 of 133) of all the nesting buteos in 1976, whereas on an area of about 20 km² 24 km north of the study area, red-tailed hawks constituted 43% (3 of 7) of all nesting buteos and ferruginous hawks 14% (1 of 7). Although the latter sample size is small, I believe the trend is real. Ferruginous hawks were never

seen while travelling north from the study area whereas Swainson's and red-tailed hawks were numerous. This suggests that the study area is very near the northern edge of the ferruginous hawk's breeding range and that red-tailed hawks nest primarily north of the study area where trees are more abundant. Secondly, ferruginous, Swainson's, and red-tailed hawks differ in nest site characteristics suggesting that the species use different habitat. Ferruginous hawks build their nest of large sticks which they presumably collect from the ground whereas Swainson's hawks and red-tailed hawks use small sticks which they probably break from trees (Dunkle 1977) since they often appear fresh. Furthermore ferruginous hawks line their nests primarily with sod and dung, Swainson's hawks with fresh forbs and leaves and red-tailed hawks with bark (Fig. 14). The nest material used by ferruginous and Swainson's hawks differs significantly ($\chi^2=160$, $P<0.005$), the sample size for red-tailed hawks was too small to allow statistical comparison. All three species also differ significantly (Duncan's multiple range test, $P<.05$) both in the height above ground at which their nests were found and the height of trees selected for nesting (Fig. 15). Nests of Swainson's hawks tend to be lowest to the ground and they nest in smaller trees or shrubs. Ferruginous hawks are intermediate and red-tailed hawks tend to nest highest and in the tallest trees. Each species probably selects the tallest trees available. However red-tailed hawks do not

Figure 14. Materials used by ferruginous (dark bars), Swainson's (open bars) and red-tailed hawks (crosshatched bar) to line their nests (both years combined).

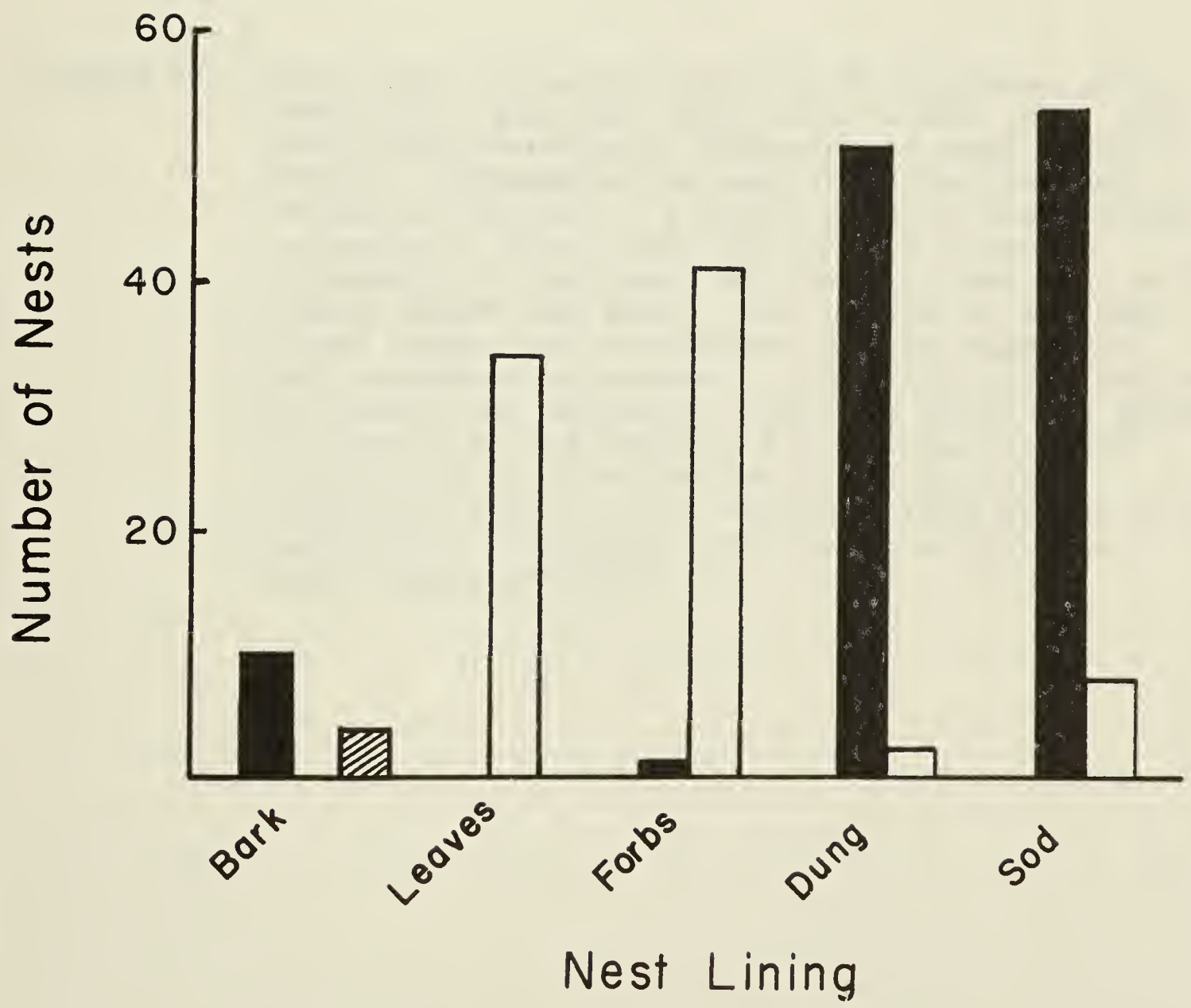
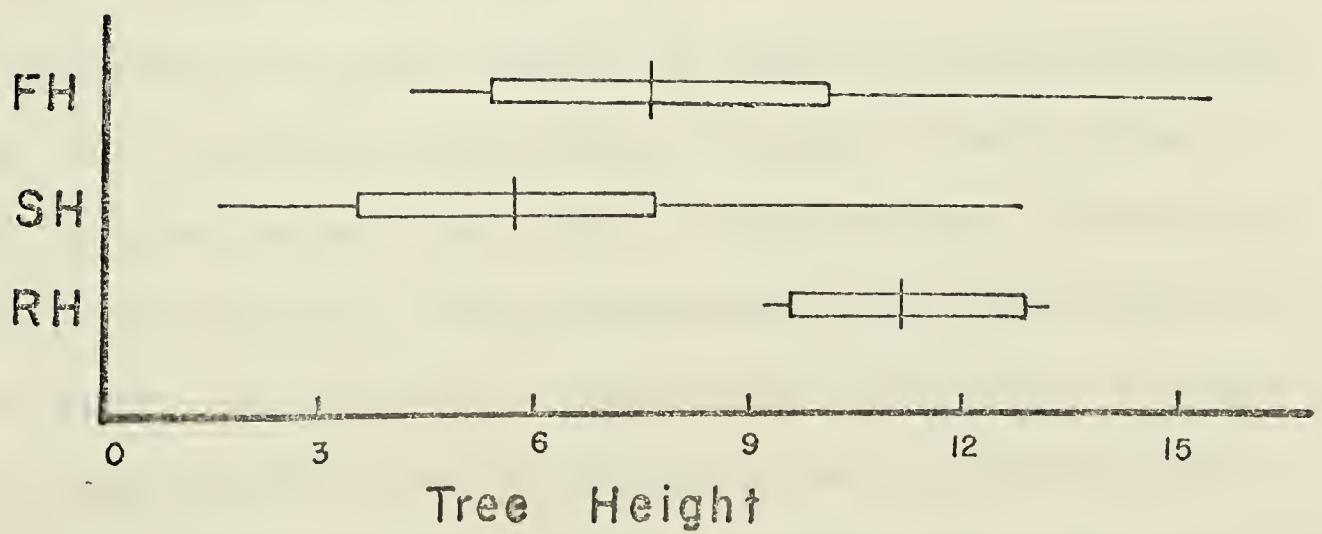
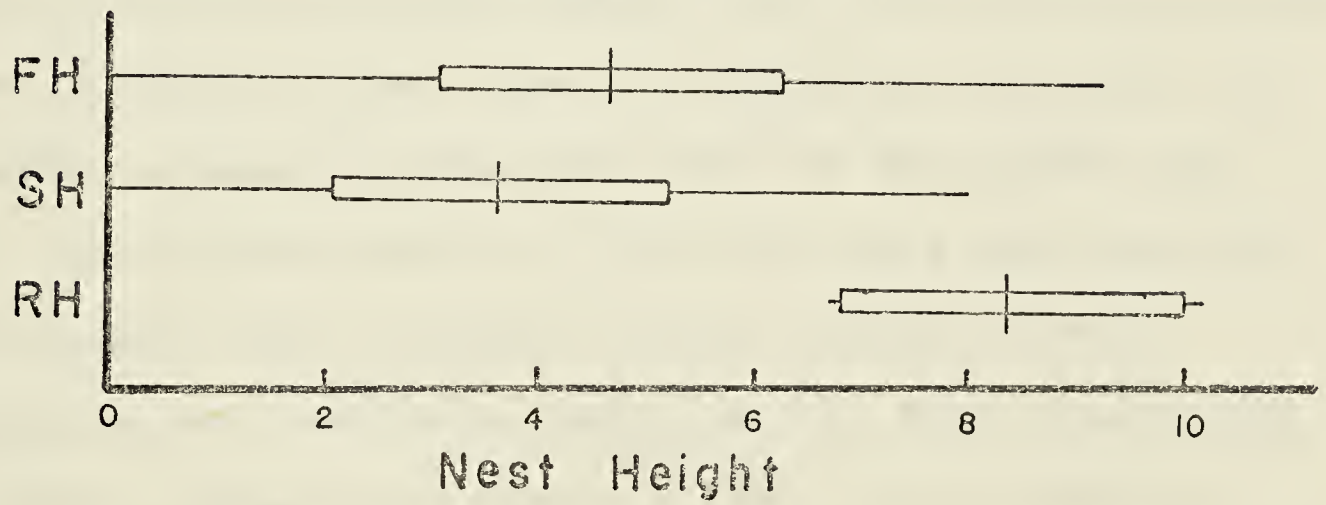
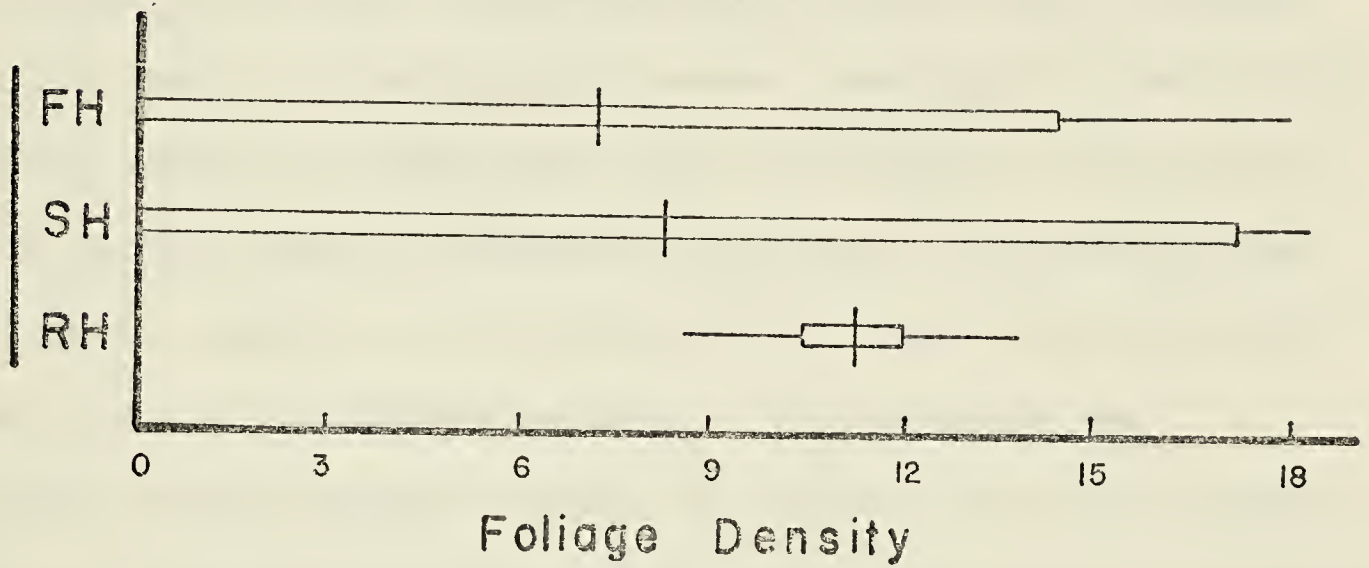
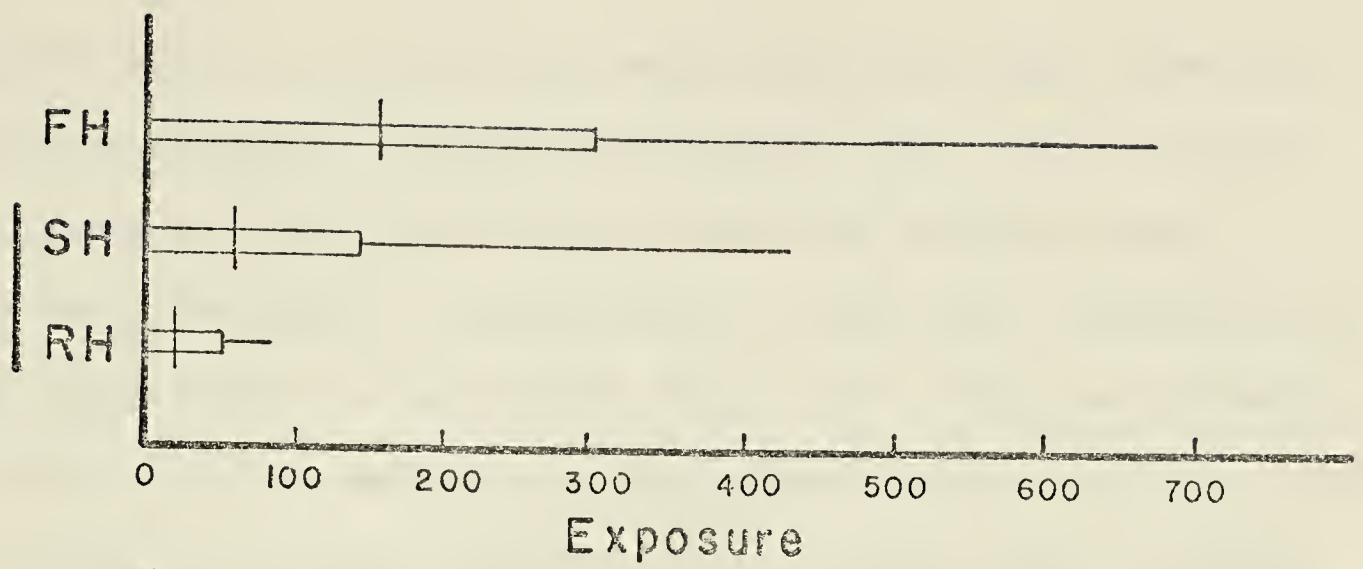
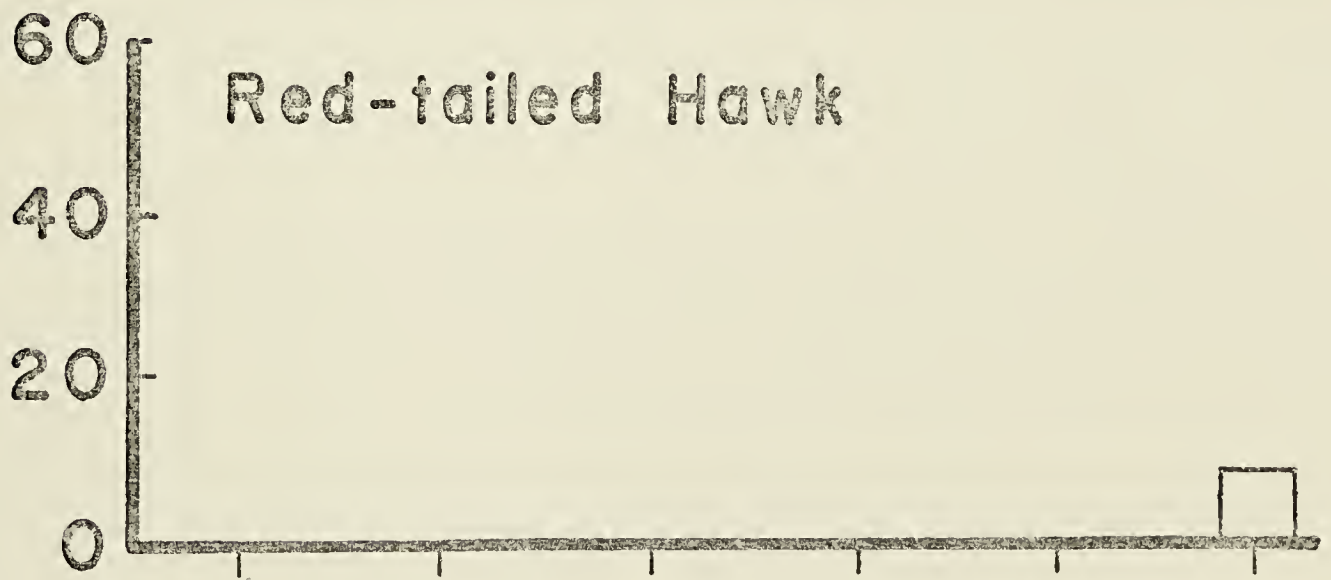


Figure 15. Nest site characteristics of ferruginous (FH), Swainson's (SH) and red-tailed hawks (RH), both years data combined. Exposure of nest sites in degrees represents the sum of horizontal and vertical exposure. Foliage density was visually determined (0[exposed] to 10[very dense foliage]) at the level of the nest and in a half circle above the nest. The height of the nest above ground and the height of the nest tree were measured in meters. Horizontal bars depict the mean, one standard deviation above and below the mean and the range. Any species differs significantly from another if it is not connected with it by a vertical line on the left (Analysis of Variance and Duncan's Multiple Range test, $p=0.05$).



appear to nest in areas where only isolated small trees or shrubs are available (Smith and Murphy 1973, Dunkle 1977). Ferruginous and Swainson's hawks nest in similar trees except that Swainson's hawks tend to nest more frequently in shrubs less than 4 m in height (Fig. 16). This is probably not related to the height, as ferruginous hawks also nest on the ground, but rather because small shrubs cannot support the bulky nests of ferruginous hawks; Swainson's hawks build a smaller nest and apparently more skillfully. Ferruginous and red-tailed hawks, although they appear to have similar food niches, appear to be ecologically segregated primarily by their use of different habitat. Ferruginous and Swainson's hawks however appear to overlap much more widely in their choice of nesting habitat but they can only both be present in habitat where trees or shrubs are available for the latter to nest in since they nest on the ground only rarely. Ferruginous hawks on the other hand nest commonly on the ground, even on gently sloping hillsides when cutbanks are not available (Murphy et al. 1969, Howard and Wolfe 1976, Lokemoen and Duebbert 1976). As a result of this difference in their choice of nesting substratum both species were probably less widely sympatric during the nesting season, before the prairie habitat was altered by man who planted trees around homesteads and facilitated the natural growth of trees by reducing the incidence of prairie fires. Ferruginous hawks probably nested throughout the prairies whereas Swainson's hawks probably were confined to

Figure 16. Nest substratum used by the three species during both years combined.



Ground Shrubs <4m Trees >1 Trees >5

areas where trees and shrubs grew naturally on the plains
such as in river valleys and around lakes.

Summarizing Discussion

The study of food habits of ferruginous, Swainson's and red-tailed hawks showed that all three species preyed primarily on Richardson's ground squirrels. The dietary overlap in prey biomass between ferruginous and Swainson's hawks was 82 and 98% in two years. There was no evidence that potential competition for food was being reduced by hunting at different times or by exhibiting different hunting methods. Despite the high degree of overlap in the use of food resources there was no evidence that ferruginous and Swainson's hawks were competing for food since the amounts of food required to raise their young appeared to be readily available. It is probable that overlap in diet is characteristically greater during the summer season because prey is reproducing and therefore more abundant at this time (Holmes and Pitelka 1968). If ferruginous and Swainson's hawks are adapted to exploit different food resources, it is possible that, under conditions of reduced food availability, both species would have exhibited a greater tendency to exploit these different resources. However, there was no evidence of any such difference during the nestling stage over the two years of this study. Outside the nestling period, particularly in fall and spring, potential differences in resource use by these two species may be much more critical to avoid competition. Ferruginous

and Swainson's hawks are not sympatric on their wintering range. However, ferruginous and red-tailed hawks, though they tend to occupy different habitat during the nesting season, overlap broadly in their wintering range and competition for food between them may be important at this time. Bock and Lepthien (1976) have suggested that these two species occupy different habitat on their wintering range.

Swainson's hawks initiate nesting later than ferruginous and red-tailed hawks but it is doubtful that this is a result of competitive displacement since it would be disadvantageous to the later breeding species to initiate nesting at a time when the food supply has already been reduced by the earlier breeding species. The initiation of breeding seems to be related to peak abundance of food (Lack 1966). This may suggest that Swainson's hawks initiate their breeding to coincide with abundance of other prey which was either not available on the study area or not exploited as a result of the abundance of Richardson's ground squirrels as prey. Young ferruginous hawks hatched at about the time of emergence of young Richardson's ground squirrels which varied considerably in the two years of this study.

Ferruginous and Swainson's hawks appear to maintain mutually exclusive intraspecific nesting territories. It also appears that their breeding densities were limited by territorial behavior since food was abundantly available and

not all nest sites, both natural and artificial, were occupied. Densities of buteos appear to be maintained at a level at which less than 15% of the available main prey is exploited which suggests that territoriality is important primarily for space and only secondarily for food (Murray 1971, Welsh 1975). Although intraspecific territories are maintained, interspecifically ferruginous and Swainson's hawks nest very close together. As a result of this close proximity, there appears to be interspecific conflict. Close nesting pairs have a higher chance of nesting failure and some pairs of ferruginous hawks appear to have been displaced by the more aggressive Swainson's hawks. Therefore, some competition between ferruginous and Swainson's hawks does exist for the space that contains a nest site and in which a breeding pair carries out nesting activities.

The use of resources by ferruginous and Swainson's hawks seems to be nearly identical which is contrary to the principle of competitive exclusion which predicts that closely-related sympatric species must exhibit some degree of ecological segregation in order to coexist (Lack 1971). Coexistence is apparently possible because each species maintains its population at a level at which the resources are still sufficiently abundant to allow two species to exist in sympatry without seriously competing for food. However, this does not seem to be the typical situation because the choice of nesting habitat, exhibited by all

three species on the study area reflects a tendency to occupy different nesting habitat. Red-tailed hawks tend to nest only in areas where tall stands of trees are available (Dunkle 1977). Ferruginous hawks, a ground-nesting species, typically inhabit open plains and arid regions nesting in trees where they are available. Swainson's hawks, a tree nesting species, is therefore unable to invade treeless plains for nesting but is limited to nesting in habitat surrounding the plains or on shrub- and tree-bordered rivers and lakes (Brown and Amadon 1968). The three species therefore are segregated by habitat during the nesting season , having only a narrow range of sympatry. This area of sympatry has recently been expanded by man who has planted trees for windbreaks and reduced the occurrence of prairie fires which would naturally impede the growth of trees in prairie habitat.

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Appendix 1. List of species of vertebrates encountered on the study area during the summer period.

Reptiles

Garter Snake (Thamnophis spp.)

Amphibians

Tiger Salamander (Ambystoma tigrinum)

Birds

Western Grebe (Aechmophorus occidentalis)

Horned Grebe (Podiceps auritus)

Eared Grebe (Podiceps caspicus)

White Pelican (Pelecanus erythrorhynchos)

Canada Goose (Branta canadensis)

Mallard (Anas platyrhynchos)

Pintail (Anas acuta)

Gadwall (Anas strepera)

American Widgeon (Anas americana)

Northern Shoveler (Anas clypeata)

Blue-winged Teal (Anas discors)

Appendix 1. (Cont.)

Cinnamon Teal (Anas cyanoptera)
 Green-winged Teal (Anas crecca)
 Canvasback (Aythya valisineria)
 Lesser Scaup (Aythya affinis)
 Ruddy Duck (Oxyura jamaicensis)
 Common Merganser (Mergus merganser)
 Harrier (Circus cyaneus)
 Ferruginous Hawk (Buteo regalis)
 Red-tailed Hawk (Buteo jamaicensis)
 Swainson's Hawk (Buteo swainsoni)
 Prairie Falcon (Falco mexicanus)
 Merlin (Falco columbarius)
 Sharp-tailed Grouse (Pedioecetes phasianellus)
 Ring-necked Pheasant (Phasianus colchicus)
 Gray Partridge (Perdix perdix)
 Great Blue Heron (Ardea herodias)
 Black-crowned Night Heron (Nycticorax nycticorax)
 Sora (Porzana carolina)
 American Avocet (Recurvirostra americana)
 Killdeer (Charadrius vociferus)
 Long-billed Curlew (Numenius americanus)
 Marbled Godwit (Limosa fedoa)
 Upland Sandpiper (Bartramia longicauda)
 Willet (Catoptrophorus semipalmatus)
 Yellowlegs (Totanus sp.)
 Short-billed Dowitcher (Limnodromus griseus)

Appendix 1. (Cont.)

Wilson's Phalarope (Steganopus tricolor)
California Gull (Larus californicus)
Ring-billed Gull (Larus delawarensis)
Franklin's Gull (Larus pipixcan)
Common Tern (Sterna hirunda)
Black Tern (Chlidonias niger)
Mourning Dove (Zenaidura macroura)
Great Horned Owl (Bubo virginianus)
Long-eared Owl (Asio otus)
Short-eared Owl (Asio flammeus)
Burrowing Owl (Athene cunicularia)
Saw-whet Owl (Aegolus acadicus)
Belted Kingfisher (Megaceryle alcyon)
Common Flicker (Colaptes auratus)
Eastern Kingbird (Tyrannus tyrannus)
Western Kingbird (Tyrannus verticalis)
Horned Lark (Eremophila alpestris)
Barn Swallow (Hirundo rustica)
Bank Swallow (Riparia riparia)
Black-billed Magpie (Pica pica)
Common Crow (Corvus brachyrhynchos)
Brown Thrasher (Toxostoma rufum)
American Robin (Turdus migratorius)
Mountain Bluebird (Sialia currucoides)
Sprague's Pipit (Anthus spragueii)
Loggerhead Shrike (Lanius ludovicianus)

Appendix 1. (Cont.)

Common Starling (Sturnus vulgaris)
 Yellow-rumped Warbler (Dendroica coronata)
 Blackpoll Warbler (Dendroica striata)
 House Sparrow (Passer domesticus)
 Western Meadowlark (Sturnella neglecta)
 Yellow-headed Blackbird (Xanthocephalus xanthocephalus)
 Red-winged Blackbird (Agelaius phoeniceus)
 Brewer's Blackbird (Euphagus cyanocephalus)
 Common Grackle (Quiscalus quiscula)
 Brown-headed Cowbird (Molothrus ater)
 Rufous-sided Towhee (Pipilo erythrophthalmus)
 Savannah Sparrow (Passerculus sandwichensis)
 Lark Bunting (Calamospiza melanocorys)
 Vesper Sparrow (Pooecetes gramineus)
 Clay-colored Sparrow (Spizella pallida)
 Brewer's Sparrow (Spizella breweri)
 White-crowned Sparrow (Zonotrichia leucophrys)
 Song Sparrow (Melospiza melodia)
 Chestnut-collared Longspur (Calcarius ornatus)

Mammals

Shrews (Sorex spp.)
 Bats (Chiroptera)
 White-tailed Jack Rabbit (Lepus townsendii)

Appendix 1. (Cont.)

Richardson's Ground Squirrel (Spermophilus richardsonii)

Thirteen-lined Ground Squirrel (Spermophilus
tridecemlineatus)

Beaver (Castor canadensis)

Deer mice (Peromyscus sp.)

Muskrat (Ondatra zibethicus)

Sagebrush Vole (Lagurus curtatus)

Meadow Vole (Microtus pennsylvanicus)

Prairie Vole (Microtus ochrogaster)

Western Jumping Mouse (Zapus princeps)

Porcupine (Erethizon dorsatum)

Coyote (Canis latrans)

Red Fox (Vulpes fulva)

Ermine (Mustela erminea)

Long-tailed Weasel (Mustela frenata)

Badger (Taxidea taxus)

Striped Skunk (Mephitis mephitis)

Mule Deer (Odocoileus hemionus)

Whitetail Deer (Odocoileus virginianus)

Pronghorn (Antilocapra americana)

Appendix 2. Mean weights of prey items used in the calculations of prey biomass. For items identified from pellets, a mean of their respective group was used.

Prey Item	Mean Weight (g)
<u>S. richardsonii</u>	
May	
Adult Males	337
Adult Females	280
Adult Sex Unknown	309
Juvenile Males	75
Juvenile Females	73
Juvenile Sex Unknown	74
June	
Adult Males	401
Adult Females	273
Adult Sex Unknown	337
Juvenile Males	180
Juvenile Females	159
Juvenile Sex Unknown	170
Age Unknown, Males	290
Age Unknown, Females	216
Age Unknown, Sex Unknown	177
July	
Adult Males	443
Adult Males	328
Adult Sex Unknown	386
Juvenile Males	268

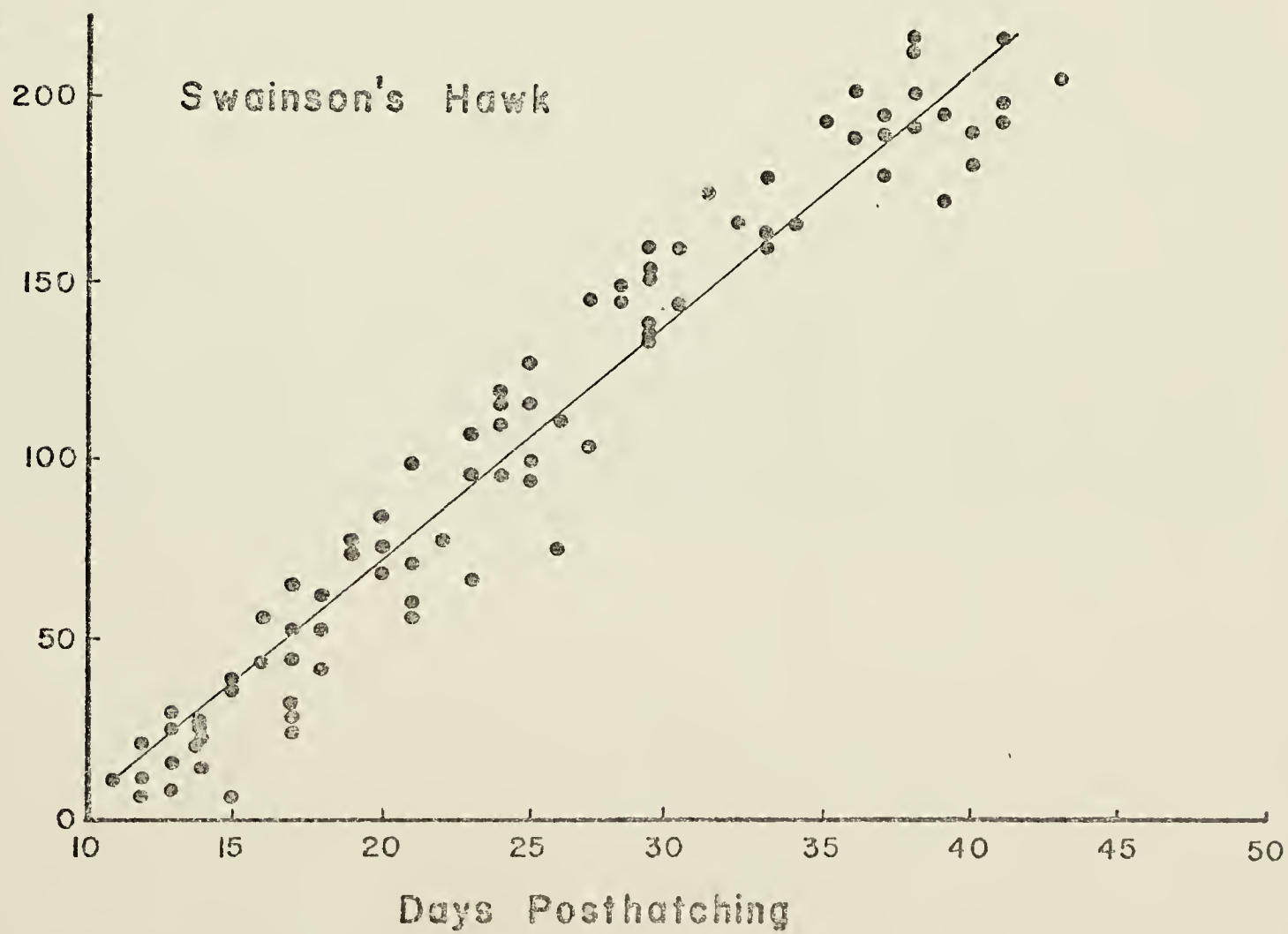
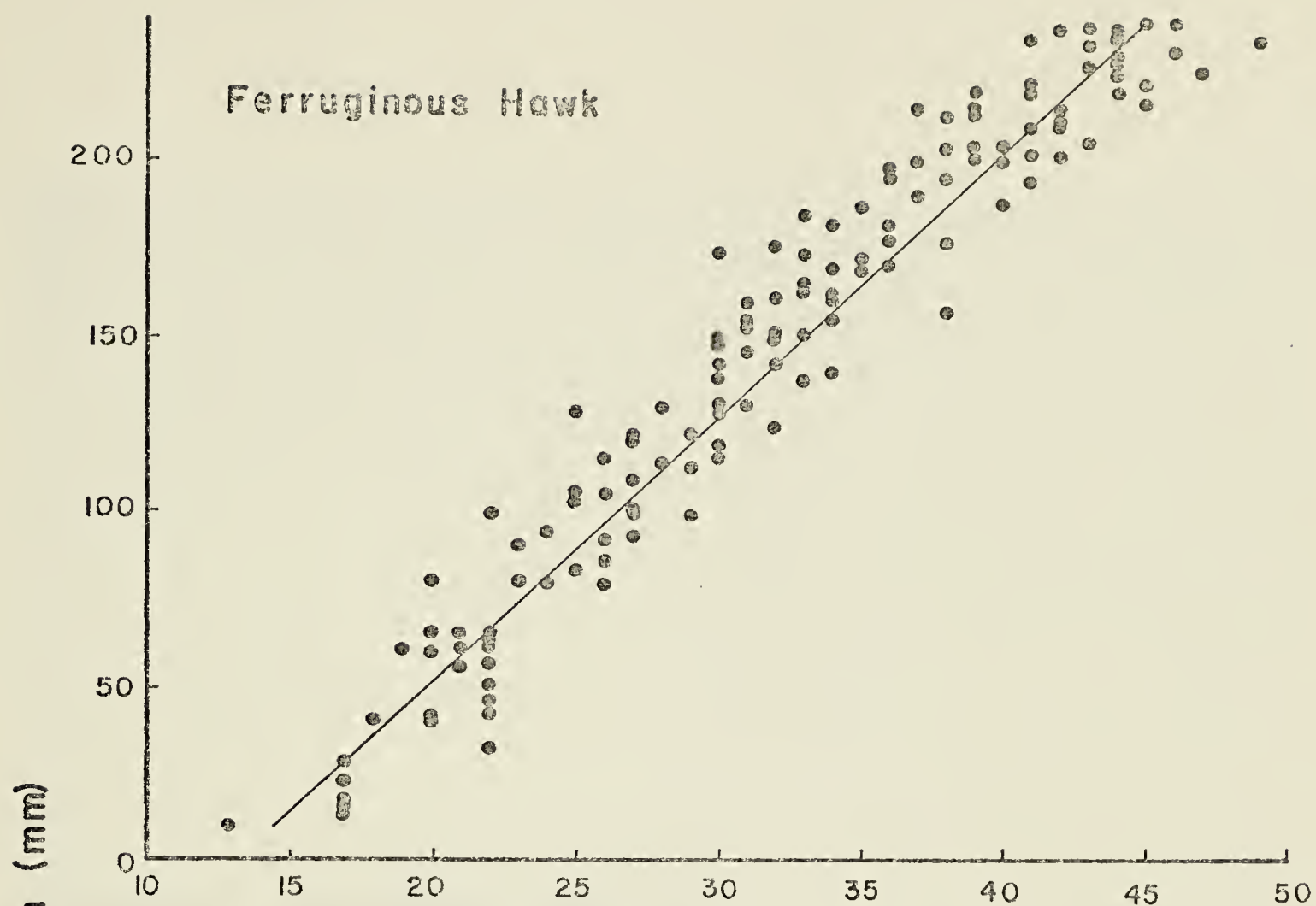
Appendix 2. (Cont.)

Juvenile Females	238
Juvenile Sex Unknown	253
Age Unknown, Males	261
Age Unknown, Females	283
Age Unknown, Sex Unknown	272
August	
Adult Females	328
Adult Sex Unknown	386
Juvenile Males	303
Juvenile Females	272
Juvenile Sex Unknown	165
Age Unknown, Males	303
Age Unknown, Females	300
Age Unknown, Sex Unknown	301
Mean of <u>S. richardsonii</u>	216
<u>S. tridecemlineatus</u>	121
<u>Microtus</u> sp.	26
<u>L. curtatus</u>	25
<u>Peromyscus</u> sp.	21
<u>Z. princeps</u>	17
Mean of Voles and Mice	22
<u>O. zibethicus</u>	770
<u>Sorex</u> sp.	6
<u>L. townsendii</u>	
Taken by <u>B. regalis</u> (Hind Foot = 80 mm)	750
Taken by <u>B. swainsoni</u> (Hind Foot = 107 mm)	2100

Appendix 2. (Cont.)

<u>M. erminea</u>	98
Anseriformes	
Adult	565
Juvenile	39
Galliformes	250
Charadriiformes	250
Passeriformes	70
Mean Weight of Aves	
Taken by <u>B. regalis</u>	182
Taken by <u>B. swainsoni</u>	145
<u>Thamnophis</u> spp.	71
<u>A. tigrinum</u>	43
Insecta	0

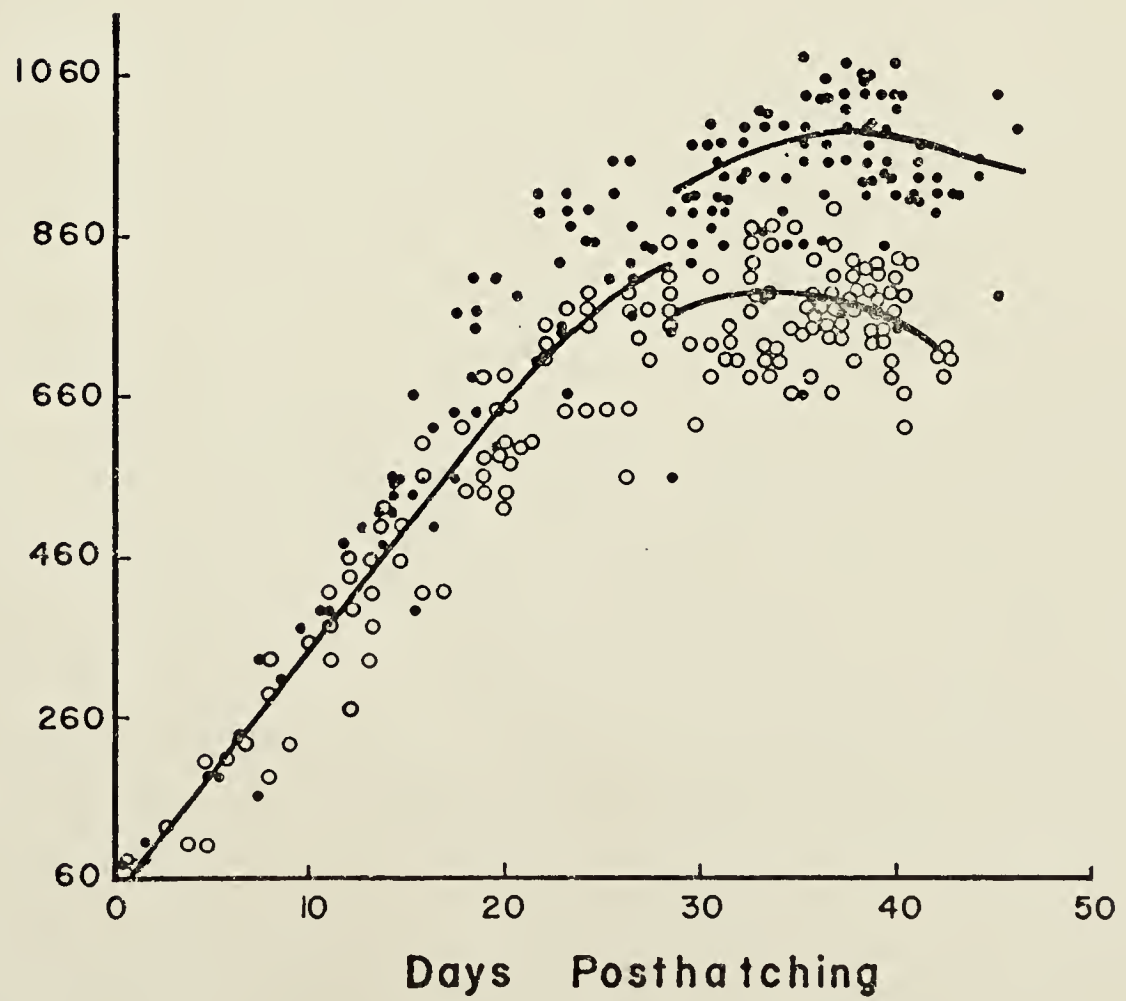
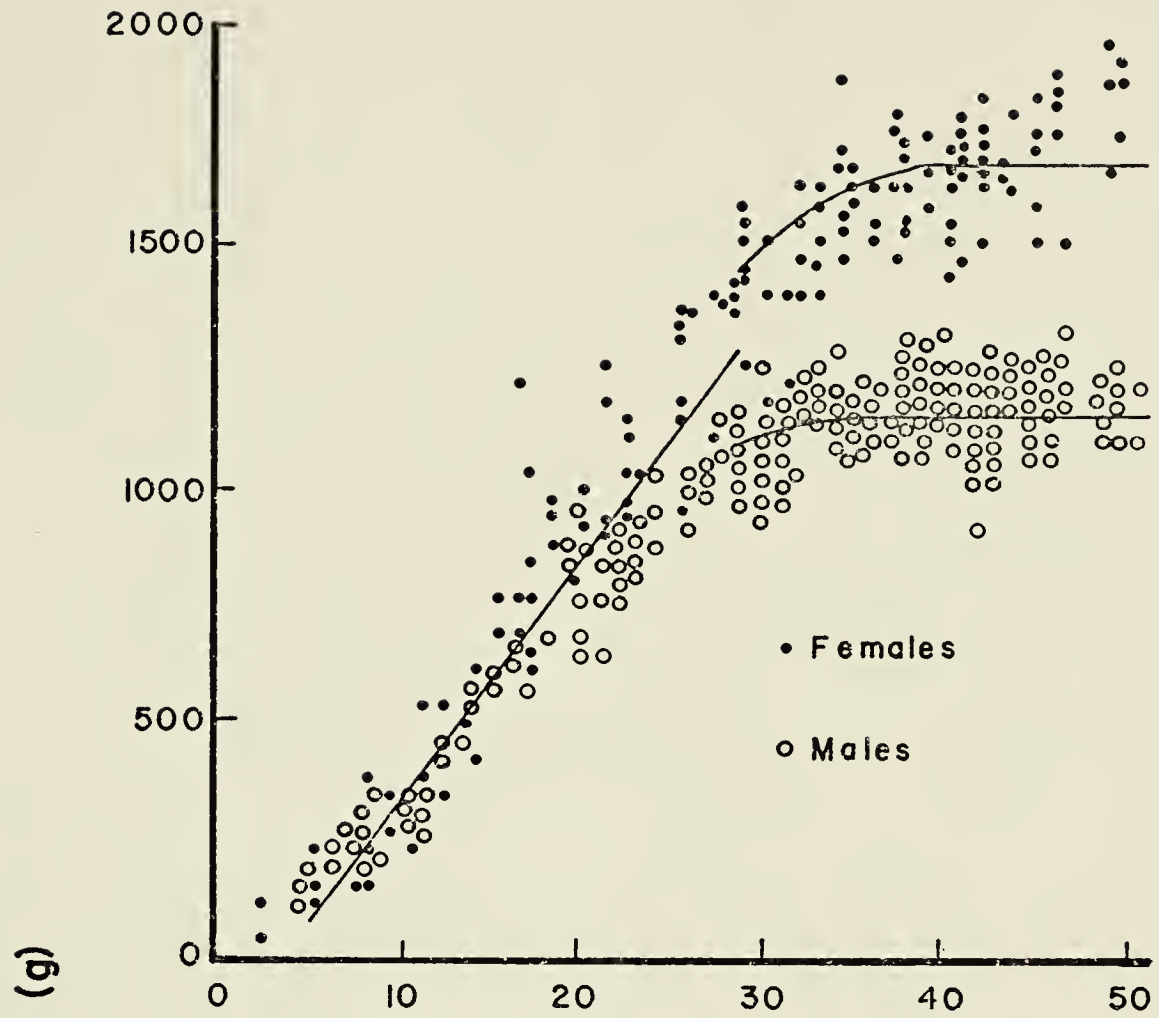
Appendix 3. Growth of primary remex number four of nestlings for which the hatching date was known to plus or minus 3 days.



Appendix 4. Artificial nest site.



Appendix 5. Method employed to correct for the inherent difference in the body weight of nestlings to allow analysis between body weight and proximity of nesting pairs. The weight of nestlings was plotted against their age. The plotted weights of ferruginous hawks show a clear difference between the two sexes after 31 days of age, the heavier nestlings are assumed to be females, the lighter ones males. The weights of nestling Swainson's hawks of different sexes are not so clearly distinct. Any nestling of Swainson's hawks with a peak weight greater than 950 g was considered a female, those less than 900 g a male. Nestlings that were weighed only once were excluded if their weight was between 850 and 900 g. The sex of nestlings weighed when less than 31 days old (ferruginous hawks) and less than 29 days old (Swainson's hawks) could not be determined. A mean growth rate was fitted to the points plotted for each sex of each species. A weight index was calculated for each nestling using its peak weight relative to the mean weight of its respective sex at equivalent age. For nestling ferruginous hawks less than 31 days old and Swainson's hawks less than 29 days old, a mean growth curve for both sexes was used.



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